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INFLUENCE OF INBREEDING ON THE CARABELLI TRAIT IN A HUMAN ISOLATE

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ABSTRACT The purpose of this study is to evaluate the influence of increased homozygosity due to inbreeding on the phenotypic distribution of the Carabelli trait. The sample consisted of 224 dental casts representing 20.2% of the total children aged 7 to 14 years from the endogamous, inbred population of the Island of Hvar, Croatia. Inbreeding analysis compared the children with different rates of grandparental endogamy relative to the expression of Carabelli's trait. The design evaluated the effect of inbreeding on Carabelli trait on the maxillary permanent first molar within a natural setting of reduced variability of environmental factors.

Very high frequency of the Carabelli trait was observed for the permanent first molar on both sides of the arcade (84% and 86% on left and right sides). Significant difference among the groups who have different degrees of inbreeding was found when Carabelli trait was divided into absent, negative features, and a positive cusp using Dahlberg's grading system.

It seems that Carabelli's trait is strongly genetically determined, and present findings imply it may be controlled byrecessive alleles. If heterogeneous polygenic developmental modules are responsible for the diversity of Carabelli's trait, they stay relatively stable after initiation of the developmental process when it appears that other environmental factors have no measurable effect. *Dental Anthropology* 2003;16(3):65-72.

The Carabelli trait is a well-known morphological feature positioned at the mesiolingual surface of maxillary molars and the trait is expressed along a continuum of a wide range of pits, crescents, grooves and cusps. Carabelli's trait is most commonly observed in European populations where frequencies vary from 50% to 90% (Laatikanen and Ranta, 1996).

Kiesser and van der Merwe (1984) evaluated the classificatory reliability of four grading systems that have been described in the literature, showing Dahlberg's eight-grade classification to be the most confidently applied. In general, Carabelli traits can be divided into two main groups: positive features (protuberance and cusp-form structures) and negative features (furrow and pit-form structures), with few morphological variations in both groups (Alvesalo *et al*., 1975; Townsend and Brown, 1981; Laatikanen and Ranta, 1996). This classification commonly has been used in interpopulation analyses (Alvesalo et al., 1975).

Although most authors agree that the Carabelli trait is genetically determined, the basis of inheritance is still not clear. Some twins studies suggest that the heritability of the trait is low (Biggerstaff, 1973; Alvesallo *et al*., 1975; Scott and Potter, 1984), whereas other results suggest high heritability (Škrinjarić, 1985; Townsend and Martin, 1992). Early studies proposed a single-gene, autosomal dominant genetic model (Dietz, 1944) and an intermediate two-allele mode of inheritance (Kraus, 1951). A polygenetic model was suggested after phenotypes were compared with the expected Hardy-Weinberg distribution (Goose and Lee, 1971).

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The trait occurs mostly bilaterally with symmetrically expressed grades (Alvesalo et al., 1975; Thomas et al., 1986; Laatikainen and Ranta, 1996), and, in asymmetric situations, no directional asymmetry has been detected (Townsend and Martin, 1992). These same authors suggest a genetic basis for the fluctuating trait asymmetry as a consequence of developmental instability, namely the degree of individuals' heterozygosity in the population (Townsend and Martin, 1992). Hence, it should be of interest to analyze a population with high homozygosity and to compare the phenotypic trait distributions and the degree of trait symmetry among its subpopulations defined by degree of homozygosity.

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TABLE 1. Age distribution of the sample

Age (years)	Total children n	Total children %	Sample n	Sample %	Sampled proportion of the total children %
7	129	11.6	27	12.0	20.9
8	153	13.8	34	15.2	22.2
9	125	11.3	28	12.5	22.4
10	117	10.6	21	9.4	17.9
11	143	12.9	26	11.6	18.2
12	136	12.3	27	12.1	19.9
13	168	15.1	28	12.5	16.7
14	138	12.4	33	14.7	23.9
Total	1109	100.0	224	100.0	20.2

An appropriate data set for such analysis is a well-investigated population divided into subpopulations that share similar environmental conditions. During 30 years of continuous interdisciplinary investigation of the rural population of the Adriatic island of Hvar different biomedical, sociocultural, biocultural, genetic and orofacial traits have been studied (Rudan, 1972; Rudan *et al*., 1982a,b, 1986; Roguljić *et al*., 1997; Janićijević, 1994; Smolej, 1987; Sujoldžić, 1997; Šimić and Rudan, 1990; Šimić *et al*., 1992; Martinović *et al*., 1998; Waddle et al., 1998). Population structure studies (Roguljić *et al*., 1997; Rudan *et al*. 1990) indicate notably high levels of inbreeding, endogamy, and isonymous marriages (marriages between individuals sharing the same surname) on this island, thus identifying the population of Hvar as one of the last genetic isolates in Europe. Such a population is an interesting model for orofacial genetic analyses because the main genetic consequence of inbreeding is to increase the proportion of homozygotes in the population (Bodmer and Cavalli-Sforza, 1976). If some recessive genes are responsible for phenotypic trait expression, prevalence of such expression is expected to be higher in an inbred than in the general population. Therefore, the aim of this study was to evaluate the influence of elevated homozygosity on the phenotypic distribution of Carabelli's trait on the permanent first molar.

MATERIALS AND METHODS

The material for this investigation consisted of 224 dental casts of children aged 7 to 14 years from all elementary schools on the island of Hvar, Croatia (Tables 1 and 2). The sample was targeted, matched for age and sex distribution to the total elementary school population of the island, and the sample covered 20.2% of the total cohort. The pupils' parents provided complete two-generation genealogical data for each examined child (*i.e.*, parents and grandparents with the place of residence of each individual). Table 1 presents the distribution of the sample according to sex, age, birthplace, and grandparental endogamy.

Dahlberg's classification was used with the following gradations: (0) smooth mesiobuccal crown surface; (1) small vertical ridge and groove; (2) small pit with minor grooves diverging from depression; (3) double vertical ridges or slight and incomplete cusp outline; (4) Y-form (*i.e.*, moderate grooves curving occlusally in opposite directions); (5) small tubercle; (6) broad cusp outline with a moderate tubercle, and (7) large tubercle with a free apex (Kieser and van der Merwe, 1984). In Dahlberg's classification, four grades (1 through 4) can be termed negative and three grades (5 through 7) positive trait forms. Asymmetry was expressed in terms of the proportion of individuals showing differences be-

TABLE 2. Sex and demographic distribution[1]

Location	Inhabitances on island under 15 years of age: Males	Females	Total		Sample Size: Males	Females	Total	
Towns	766	711	1477	69.6%	86	68	154	68.8%
Villages	339	305	644	30.4%	40	30	70	31.2%
Total	1105	1016	2121		126	98	224	
	52.1	47.9%			56.3%	43.7%		

[1]There are three towns on the island of Hvar: Hvar, Starigrad and Jelsa. These towns are administrative centers for a number of villages around the island, and the majority of inhabitants on the island live in these centers.

TABLE 3. Distribution of left Carabelli trait according to Dahlberg's classification

	Grade of Carabelli's Trait								
	0	1	2	3	4	5	6	7	Total
Outbred									
Number	5	1	6	0	0	2	0	0	14
Percent	35.7	7.1	42.9	0.0	0.0	14.3	0.0	0.0	
Low inbreeding									
Number	19	14	17	9	34	23	9	1	126
Percent	15.1	11.1	13.5	7.1	27.0	18.3	7.1	0.8	
High inbreeding									
Number	4	5	12	3	14	16	5	2	61
Percent	6.6	8.2	19.7	4.9	23.0	26.2	8.2	3.3	
Total									
Number	28	20	35	12	48	41	14	3	201
Prcent	13.9	10.0	17.4	6.0	23.9	20.4	7.0	1.5	

tween sides as described by Kieser (1984).

Inbreeding analysis compared the children based on three rates of grandparental endogamy (i.e., grandparents born in the same settlement). One, an outbred group (some grandparents were not from the island). Two, a group with "low inbreeding" (one or two grandparents born in the same village). Three, a group with "high inbreeding" (all four grandparents born in the same village). This was done across all studied villages. Several previous studies in Hvar showed that complete grandparental endogamy is a reliable indicator of inbreeding in these small villages, as most (if not all) individuals will eventually be related at some point in history (Rudan and Rudan, 2000; Smolej-Narančić and Rudan, 2001). Thus, complete endogamy in these populations in some instances carries greater potential to discriminate inbred from non-inbred individuals than the actual genealogical reconstruction, because the latter tends to underestimate the remote component of inbreeding (Broman and Weber, 1999; Shifman and Darvasi, 2001). The present study design was to evaluate the effect of inbreeding on Carabelli's trait at the individual level. The study has the benefit of reduced environmental variance across studied villages, a feature that has been documented previously (Rudan *et al*., 1999).

The statistical significance of the differences in frequencies was evaluated using a chi-square test, and symmetry was evaluated using the Wilcoxon test with alpha level set at 0.10 and at 0.05. Pearson chi-square value, likelihood ratio and linear-by-linear association

TABLE 4. Distribution of right Carabelli trait according to Dahlberg's classification

	Grade of Carabelli's Trait								
	0	1	2	3	4	5	6	7	Total
Outbred									
Number	5	1	5	1	0	2	0	0	14
Percent	35.7	7.1	35.7	7.1	0.0	14.3	0.0	0.0	
Low inbreeding									
Number	19	14	13	16	34	17	10	1	124
Percent	15.3	11.3	10.5	12.9	27.4	13.7	8.1	0.8	
High inbreeding									
Number	7	4	10	4	12	14	7	1	59
Percent	11.9	6.8	16.9	6.8	20.3	23.7	11.9	1.7	
Total									
Number	31	19	28	21	46	33	17	2	197
Prcent	15.7	9.6	14.2	10.7	23.4	16.8	8.6	1.0	

TABLE 5. *Statistical tests for data from the left side*

Statistic	Value	df	P
Chi-Square	23.944*	14	0.047
Likelihood Ratio	26.689	14	0.021
Mantel-Haentzel	9.662	1	0.002

*12 cells (50.0%) have expected counts less than 5. The minimum expected count is 0.21.

were presented after testing inter-group differences. Likelihood ratio is a goodness-of-fit statistic similar to Pearson's chi-square and equivalent to it in large sample sizes—with the advantage that it can be subdivided into interpretable parts that add up to the total. Linear-by-linear association (*i.e.*, the Mantel-Haenszel chi-square test) is a measure of linear association between the row and column variables.

RESULTS

Trait expression

Tables 3 and 4 show the distributions of Carabelli's trait on the left and right first molars in the outbred sample, and the samples with low and high inbreeding. All distributions varied significantly in frequency between groups (P < 0.05) for each side of the arch (Tables 5 and 6). In the outbred group, grade 0 on the right side and 0 and 2 on the left side occurred most frequently. In the sample with inbreeding, grade 4 (group with low inbreeding) and 5 (group with high inbreeding) were most common.

Chi-square tests (Tables 5 and 6) disclosed statistically significant differences among the groups (P < 0.05 for left side and 0.10 > P > 0.05 for right side) with different degrees of inbreeding when Carabelli's trait was divided into absent, negative, and positive expressions. Positive trait expression was observed in 14% of the individuals in the outbred group, 23-26% with low inbreeding, and 37-38% with high inbreeding. Absence of the trait was observed in 36% of the outbred individuals but only 7-12% of individuals with high inbreeding.

Trait symmetry

The distribution of the grades in 197 individuals is shown in Table 7. Significant correlation (P < 0.001) was observed between the sides of the jaw (Table 8). No individual showed a positive cusp on one side and absence of the character on the other. However, twelve individuals (5%) showed a negative expression unilaterally, with no trait on the other side.

TABLE 6. *Statistical tests for data from the right side*

Statistic	Value	df	P
Chi-Square	21.988*	14	0.079
Likelihood Ratio	24.312	14	0.042
Mantel-Haentzel	7.138	1	0.008

*10 cells (41.7%) have expected counts less than 5. The minimum expected count is 0.14.

Table 9 shows the distribution of Carabelli's trait according to Dahlberg's classification, and Table 10 shows the left-right concordance according to the negative and positive expressions among the individuals with different inbreeding levels. No significant difference was found among the groups (Table 11). Using Dahlberg's classification, inbred individuals were more symmetric than those from the outbred group. The opposite finding was observed when comparing a negative and a positive expression, namely more asymmetric expressions occurred in inbred groups.

DISCUSSION

The highly endogamous population of Hvar is characterized by a very high frequency of Carabelli's trait. The overall frequency was 84% on the right side and 86% on the left side. This is approximately the same as the highest frequency of the trait reported by Kirveskari (1974) among Skolt Lapps (90%). A positive cusp was observed in 29% of individuals on the left side and 26% on the right side, which is somewhat higher than the value observed among Skolt Lapps (20%) and is almost equal to findings by Townsend and Martin (1992) in a sample of Caucasian twins and to the frequency in the German population (30%) reported by Reiners-Karsch (1964). A higher frequency of the cusp has only been reported by Keene (1968) among north-American military recruits (38%).

The literature illustrates that inbreeding can affect orofacial traits. Direct evidence for the influence of inbreeding on orofacial traits and on syndromes has, for example, been provided by Schull and Neel (1965), Maatouk et al. (1995), and Zlotoroga (1997) on humans and by Baume and Lapin (1983) on *Papio hamadryas*. Indirect evidence for the effect of inbreeding on orofacial traits in humans can be found in studies reporting higher prevalence of various orofacial traits in small isolated consanguineous communities such as Yanomami Indians of Brazil (Pereira and Evans, 1975), the Kwaio of the Solomon Islands (Lombardi and Bailit, 1972), and Ashkenazi Jews (Ben-Bassat *et al.*, 1997). However, the Carabelli trait has not previously been the focus of inbreeding investigations.

The biologically isolated population of Hvar Island was divided into three groups in this study. First, there was a group with some grandparents who moved to the island from abroad, carrying new genes into the island's gene pool (the outbred group). This group consists of just 14 children, but this represents the actual proportion of incomers. The second and the third groups are individuals whose ancestors were born on the island. In the second group are individuals with up to two grandparents from the same village, whose inbreeding scores range from 0.0039 to 0.0156. The third group consists of individuals with three or four grandparents from the

TABLE 7. Distribution of Carabelli trait according to negative-positive dichotomy

	Left-Hand Side				Right Hand Side			
	Absent	Negative	Positive	Total	Absent	Negative	Positive	Total
Outbred								
Number	5	7	2	14	5	7	2	14
Percent	35.7	50.0	14.3		35.7	50.0	14.3	
Low inbreeding								
Number	19	74	33	126	19	77	28	124
Percent	15.1	58.7	26.2		15.3	62.1	22.6	
High inbreeding								
Number	4	34	23	61	7	30	22	59
Percent	6.6	55.7	37.7		11.9	50.8	37.3	
Total								
Number	28	115	58	201	31	114	52	197
Percent	13.9	57.2	28.9		15.7	57.9	26.4	

same village, mostly villages with an inbreeding score over 0.0156, which is representative of an extremely isolated group. Using Dahlberg's classification, absence of Carabelli's trait was the modal finding in the outbred group, while grade 4 was most common in the low-inbreeding group, and grade 5 was most common in the high-inbreeding group. Of note, there was an obvious and statistically significant *dose-response relationship* for the expression of Carabelli's cusp (Dahlberg's grade 5, 6 and 7) with the degree of inbreeding.

This association between inbreeding and trait frequency implies that the trait may be modulated by recessive genes. Rudan (2002) has noted that an increase in inbreeding of 5% corresponds to having about 1750 random genes across the genome identical by descent if the total number of human genes is between 30,000 and 40,000 (Subramanian et al., 2001). If this unrecombined homozygosity has a notable effect on Carabelli's trait frequency, two mechanisms could explain it, (1) homozygosity brings together rare major genes or (2) the genes controlling this trait are of small effect but are incredibly numerous, scattered across the genome. Genes with major effects arise after mutations that are considered to be extremely rare, because the probability of a random mutation that causes a small effect is much greater. Even if such mutations are present in some individuals, it is extremely unlikely that similar effects of inbreeding, as the high significance of linear-by-linear association indicated, would be observed in the whole group with high inbreeding and across all of the villages. It is more likely that the Carabelli trait is therefore a polygenetic trait. Moreover, as results from this study indicate, it seems that the trait is caused by a rare allelic variant rather then a common one because if the trait were caused by common allelic variants, inbreeding could not increase the frequency in the homozygotes. A large number of genes involved in the model of trait expression can be explained as a product of a dynamic developmental program manifested in the activation of the developmental modules. As Jernvall and Jung (2000) suggest, a cascade model of molar trait development includes a number of stages and can be used to explain the variation of properties of dental characters and character states related to cusp initiation. A portion of a number of genes involved in such a complex developmental model can be recognized in different and tissue-related homeobox gene expression (transcription factors responsible for activation of primary genes and direct the differentiation of whole body parts (Gilbert *et al*., 1996)).

TABLE 8. Statistical tests for data from the sides after dichotomizing the data into negative and positive trait expressions

Statistic	Value	df	P
	Right Side		
Chi-Square	10.466[a]	4	0.033
Likelihood Ratio	9.701	4	0.046
Mantel-Haentzel	8.606	1	0.003
	Left Side		
Chi-Square	9.275[b]	4	0.055
Likelihood Ratio	8.288	4	0.082
Mantel-Haentzel	6.745	1	0.009

[a]2 cells (22.2%) have expected counts less than 5. The minimum expected count is 1.95.

[b]2 cells (22.2%) have expected counts less than 5. The minimum expected count is 2.20.

Despite our expectation of significant difference of bilateral symmetry among the groups, all groups had similar distributions of bilateral asymmetry. Increased fluctuating asymmetry in the inbred group had been

*TABLE 9. Occurrence of Carabelli trait on the maxillary first molar on the two sides of the dental arcade**

		Right-hand side								
	Class	0	1	2	3	4	5	6	7	Total
Left Side	0	23	1	3						32
	1	4	9	1	5					18
	2	3	4	20		3	2	1		26
	3		3		8		1			19
	4	1	1	1	2	35	4	1		45
	5			1	3	7	23	6		34
	6				1		4	8	1	17
	7							1	1	2
	Total	28	19	33	12	45	40	14	2	193

*Kendall's tau = -0.735.

anticipated because individuals with reduced genetic heterogeneity are more sensitive to environmental stress during ontogeny (e.g., Bailit *et al*., 1970; Thornhill and Moller, 1997).

Results of left-right concordance when using Dahlberg's eight grades differ from those that lump the expressions into a positive-negative dichotomy. Dahlberg's classification is more precise and only virtually-identical expressions are recognized as bilaterally symmetric, whereas different grades of positive and negative expressions will be pooled together in the second, dichotomous classification. However, a similar symmetry distribution was observed with both classifications, rejecting the hypothesis about influence of inbreeding on fluctuating asymmetry of Carabelli's trait. If inbreeding increases the symmetry of a trait, one explanation is that different genes with recessive variants are responsible for trait expression on the left and right sides of the arcade. This explanation can be rejected here because the repeated activation of the developmental modules during tooth development suggests that homologous cusps and crests are not coded as such into the genome, but that the whole cusp pattern is a product of a dynamic program (Jernvall, 2000; Zhao et al., 2000). Obviously, high bilateral symmetry of the trait in various investigations implies that a multitude of other environmental factors during the development of the trait have no significant effect. It seems that this trait is almost completely genetically determined with a predominant genetic variance and that most of factors during odontogenesis are not environmental. Those factors, as Jernvall and Jung (2000) commented on for primate molar shapes, "do not reflect just a static genetic code readable deep inside the genome, but rather, it is a readout of the information stored in the dynamic cusp-making program." Therefore, polygenic developmental module responsible for the diversity of Carabelli trait could be variable, but it stays relatively stable after initiation of the developmental process.

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TABLE 10. Left-right symmetry of trait expression

Group	Dahlberg's Eight-Grade Scale Symmetric	Asymmetric	Total	Dichotomized Trait Expressions Symmetric	Asymmetic	Total
Outbred						
Number	3	11	14	12	1	13
Percent	21.4	78.6		92.3	7.7	
Low inbreeding						
Number	42	78	420	100	17	117
Percent	35.0	65.0		85.5	14.5	
High inbreeding						
Number	20	37	57	46	7	53
Percent	35.1	64.9		86.8	13.2	
Total						
Number	65	126	191	158	25	183
Percent	34.0	66.0		86.3	13.7	

TABLE 11. Statistical tests for left-right symmetry of trait expression

Statistic	Value	df	P
Eight-Grade Scale			
Chi-Square	1.069[a]	2	0.586
Likelihood Ratio	1.149	2	0.563
Mantel-Haentzel	0.405	1	0.525
Dichotomized Expression			
Chi-Square	0.477[b]	2	0.788
Likelihood Ratio	0.539	2	0.764
Mantel-Haentzel	0.042	1	0.837

[a]1 cell (16.7%) has expected counts less than 5. The minimum expected count is 4.76.

[b]1 cell (16.7%) has expected counts less than 5. The minimum expected count is 1.78.

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Laboratory Name Change

Ebba During reports that theArchaeoosteological Research Laboratory, Royal Castle Ulriksdal, S-17079 Solna, Sweden, has undergone a name change to a “less lumbering” title. The new name is **Osteoarchaeological Research Laboratory**. The address remains the same.

Professor During is Head of the laboratory, and she can be reached via e-mail at: ebba.during@ofl.su.se.

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Metric Analysis of Permanent and Deciduous Teeth from Bronze Age Tell Leilan, Syria

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ABSTRACT Between 1979 and 1989 the skeletal remains of 21 adults and 38 children, yielding 317 permanent and 134 deciduous teeth, were recovered at Tell Leilan, Syria, the site of a major urban center during the emergence of complex state society in northern Mesopotamia in the mid-third millennium BC. Tooth crown dimensions (faciolingual and mesiodistal diameters, total crown area, and molar crown area) are presented and the last two serve as the primary units of comparison for a diachronic interpretation of tooth size variation in the ancient Near East. Both permanent and deciduous dental data support the pattern of dental reduction since the Middle Paleolithic that has been documented for Asia and Europe. The total crown areas for the permanent and deciduous dental samples, 1189 mm^2 and 497 mm^2 respectively, place this archaeological population at the smaller end of the crown area scale for the Near East; smaller in size than nearby Paleolithic and Neolithic populations. Given the paucity of odontological data for this area, this study contributes to the odontometric history of Mesopotamia and as a summary compilation and comparison of previously conducted odontometric work as it relates to the phenomenon of dental reduction within the ancient Near East. *Dental Anthropology* 2003;16(3):73-80.

Analyses of ancient Near Eastern dentitions are sparsely represented in the literature, whether concerning pathology (*e.g.*, Krogman, 1940; Carbonell, 1966), non-metric traits (*e.g.*, Dahlberg, 1960; Rathbun, 1972), or metric variation (e.g., Macchiarelli, 1989; Rosenzweig and Zilberman, 1967, 1969). One reason for this may be that excavations of human remains at such classic sites as Kish (Mackay, 1925; Watelin and Langdon, 1934), and Ur (Wooley, 1934), were conducted in the early first half of the twentieth century, a time when studies of the teeth were not considered essential components of skeletal analysis. Unfortunately, although dental anthropological studies have become more common, the political climate of the Near East in recent decades has prevented research at many ancient Mesopotamian sites. As a consequence, some researchers have begun to explore the rich archaeological history of northern Mesopotamia, a region long ignored by archaeologists who, in the past, preferred to study agricultural origins and state emergence in the southern Iraqi floodplain. As a result of excavations conducted in northeastern Syria in the last quarter of the twentieth century, a new, albeit limited, set of archaeological human remains is available for analysis.

This paper presents the results of an odontometric analysis of human skeletal remains from the northern Mesopotamian site of Tell Leilan, Syria, and compares these results to odontometric data from other regions and time periods of the Near East in order to examine diachronic dental size variation. Documentation of dental reduction trends based on odontometric observation of archaeological populations has been achieved in a number of areas of the world for post-Paleolithic Asia (Brace, 1978; Lukacs and Hemphill, 1991) and Upper Paleolithic-Mesolithic Europe (Frayer, 1977, 1978), but more work in regions and time periods previously unexamined by dental anthropologists will enable researchers to more accurately understand the evolutionary processes involved in hominid dental reduction, one of the most widely reported, and hotly debated trends in the study of human evolution (Brace, 1963, 1964, 1978; Brace *et al*., 1987, 1991; Calcagno, 1989; Gibson and Calcagno, 1989; Kieser, 1990; Macchiarelli and Bondioli, 1984). This study, then, is intended as a contribution to the odontometric history of Mesopotamia and as a summary compilation and comparison of previously conducted odontometric work as it relates to the phenomenon of dental reduction within the ancient Near East.

MATERIALS AND METHODS

Tell Leilan is located on the fertile Habur plains of northeastern Syria. Occupied from the mid-sixth millennium BC, the site became one of the three major urban centers of Subir during the emergence of complex state society in northern and southern Mesopotamia in the mid-third millennium BC (Weiss *et al*., 1993). During the Tell Leilan IIb period (~2300-2200 BC), the imperial interests of the southern Mesopotamian ruler Sargon, and his successors, brought Tell Leilan and the rest of Subir under Akkadian domination (Gibbons, 1993; Weiss *et al*., 1993). At approximately 2200 BC, Tell Leilan was abandoned for some 300 years, due to severe

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climate change that may have resulted from volcanic eruption and subsequent desertification of cultivable land in the region (Weiss et al., 1993). This climate change has been documented in a number of areas in the eastern Mediterranean (Amiran, 1986; Frumkin et al., 1991; Otterman and Starr, 1995; Raban and Galili, 1985), and has led some scholars to reevaluate previously held theories on the collapse of state-level societies in the ancient Near East during the late third millennium BC (Issar, 1995).

The skeletal remains of 21 adults and 38 children were recovered during five seasons of excavation at Tell Leilan between 1979 and 1989 (Weiss, 1985, 1986; Weiss et al., 1993), and are presently curated at the Department of Anthropology, University of Alberta. Preservation of the skeletal remains is poor, although the dentition, when present, is in excellent condition. However, only 317 teeth out of a potential 672 permanent teeth and only 134 of a possible 760 deciduous teeth were collected during excavation. Antemortem tooth loss probably contributed to the incomplete nature of the dental sample, as did difficulties in excavation; there are many neonatal and infant remains in which many of the deciduous teeth were either unformed or incompletely formed and hard to recover. Fortunately, one or more tooth crown dimensions (*e.g.*, mesiodistal and/or faciolingual crown diameter) could be measured in 82% of the collected permanent teeth and 60% of the deciduous teeth. The remaining teeth could not be measured due to incomplete eruption, extreme occlusal wear, or postmortem crown breakage. The majority of the remains from Tell Leilan date to the urban period of third millennium occupation (~2600 to ~2200 BC), although they range in date from the early third millennium BC to the early second millennium BC. Due to the small sample sizes and relatively homogenous cultural context, however, all the remains are treated here as a sample from a single population.

The senior author took tooth crown measurements with a Helios needle-point dial caliper, calibrated to 0.05 mm. Measurements were rounded to 0.1 mm. Two measurements, maximum faciolingual (FL) diameter[1] and maximum mesiodistal (MD) diameter were taken for each tooth as described by Mayhall (2000). Intraobserver error was assessed by re-measurement of a randomly selected subset of 10% of the original sample, yielding a mean intraobserver measurement difference of 0.060 and a standard deviation of 0.22; such values are well within the ranges reported by other researchers for similar studies (Wolpoff, 1971a; Lukacs, 1985; Lukacs and Hemphill, 1991). Paired sample t-tests were used to assess FL and MD asymmetry of permanent right and left antimeres, although asymmetry was not evaluated for the deciduous sample because of its small size. Tabulation and statistical analysis of the data were completed using Excel (Microsoft Corporation, 1991) and Systat software (SYSTAT Inc., 1990-1992), respectively. The data are presented with the sexes pooled because the incomplete and fragmentary state of the skeletal remains rendered accurate assessment of sex for the Tell Leilan sample very difficult.

Crown area (CA) was calculated by multiplying the mesiodistal and faciolingual measurements for each tooth (Wolpoff, 1971b). Total crown area (TCA), the sum of mean cross-sectional crown areas for all upper and lower teeth on one side of the jaw, and molar crown area (MCA), the sum of the mean cross-sectional crown areas for upper and lower posterior teeth on one side of the jaw, serve as the primary units of comparison for diachronic interpretation of permanent tooth size variation in the ancient Near East. TCA and MCA values for the comparative samples were obtained either from published data or were calculated from published mean MD and FL crown diameters.

RESULTS

The mean differences between right and left measurements for each permanent tooth type were generated using a paired sample t-test. While there is a slight degree of directional asymmetry (with 11 of 16 teeth from the left side slightly larger, on average, than the right side), this difference is not statistically significant at alpha = 0.05.

The standard deviation of mean differences between right and left antimeres provides another useful indicator of the extent of dental asymmetry (Smith *et al.*, 1982). In contrast to the pattern that is usually observed (Lukacs and Hemphill, 1991), the Tell Leilan standard deviation does not display a trend of smaller to larger values when moving distally within a given tooth class. This is most likely caused by the small number of paired observations as well as by the large standard deviation of certain teeth (e.g., third molars). The mean standard deviation of FL and MD diameters for all teeth provides a general indication of asymmetry for the dentition as a whole (Lukacs and Hemphill, 1991); for the Tell Leilan permanent teeth, this value is 0.40, somewhat higher than that observed by other researchers (e.g. 0.23 and 0.24, Lukacs and Hemphill, 1991)[2], although Smith and co-workers (1982:283) have observed that standard deviations as large as 0.80 are not uncommon when samples of fewer than 100 individuals are used.

Crown diameters and areas are presented in Tables 1 and 2 for the left side of the dental arcade, and, because of the statistically insignificant nature of left-right antimeric differences, values from the right side have been substituted for missing left values in order to increase the number of observations for certain teeth and,

[1]"Faciolingual" is used here to encompass both labiolingual measurements of the anterior teeth and buccolingual measurements of the posterior teeth.

[2]This precludes the utilization of the mean standard deviation for the Tell Leilan permanent dentition in comparative analysis of interpopulational dental asymmetry.

TABLE 1. Mean crown diameters (in mm) and mean crown areas (in mm^2) of permanent left teeth from Tell Leilan[1]

	MAXILLA									MANDIBLE								
	Faciolingual Diameter			Mesiodistal Diameter			Crown Area			Faciolingual Diameter			Mesiodistal Diameter			Crown Area	
	n	mean	sd	n	mean	sd	mean	sd		n	mean	sd	n	mean	sd	mean	sd
I1	12	7.38	0.37	12	8.58	0.64	63.36	6.35		6	6.05	0.21	7	5.16	0.76	29.79	3.46
I2	11	6.77	0.60	11	6.46	0.42	43.94	6.44		10	6.36	0.37	11	5.48	0.76	33.99	4.82
C	10	8.63	0.46	10	7.30	0.45	64.02	5.13		9	7.92	0.53	10	6.71	0.37	52.60	3.83
P1	11	9.07	0.48	10	6.75	0.42	61.38	6.14		12	7.89	0.50	12	6.76	0.41	53.35	4.89
P2	11	9.07	0.66	11	6.53	0.43	59.43	7.81		12	8.04	0.81	12	7.03	0.62	58.69	10.46
M1	14	11.93	1.73	14	10.48	0.95	125.71	25.60		12	10.63	0.52	12	11.28	0.70	120.10	11.01
M2	11	10.85	1.07	10	9.49	1.10	103.59	19.04		11	10.43	0.47	12	11.22	0.80	115.57	11.01
M3	7	10.89	1.18	8	9.30	0.61	99.37	10.30		5	9.96	0.92	5	10.38	0.92	103.92	17.83

[1]Since left-right antimeric differences are not statistically significant, values from the right side have been substituted for missing left values; n, number of observable teeth; sd, standard deviation

thus, the utility of the statistical results. Table 1 presents the mean FL and MD crown diameters and crown areas for the Tell Leilan permanent dentition, sexes pooled. All measurements are in millimeters (mm) for crown diameters (FL and MD) and millimeters squared (mm^2) for crown areas (CA). Table 2 presents the mean FL and MD crown diameters and crown areas for both left and right antimeres in the deciduous dentition.

Numerous odontometric studies have utilized the TCA and/or the MCA for comparing tooth crown size variation (e.g., Brace, 1980; Lukacs, 1985; Brace et al., 1987), since crown areas most closely approximate the total functional occlusal size of the dentition (Wolpoff, 1971b). Thus, crown area is the trait upon which natural selection acts (Brace, 1980) making TCA and MCA, as single discrete values, highly useful for examining interpopulational variation in tooth size.

For the present study, the total and molar crown areas of the Tell Leilan permanent dental sample are compared with the total and molar crown areas from several archaeological populations in the Near East (Fig. 1), beginning in the Middle/Upper Paleolithic and ending in the Iron Age, as a rudimentary examination of tooth size reduction. Although it would be preferable to limit the diachronic comparison to sites that are specifically located within northern Mesopotamia, very few odontological studies have been conducted in the region. For this reason, crown area values for the nearest available archaeological populations in Iran, Iraq, Israel, and Turkey have been used instead.

Table 3 presents the data from sex-pooled samples for each archaeological population in the comparison.

TABLE 2. Mean crown diameters (in mm) and crown areas (in mm^2) for deciduous teeth from Tell Leilan

		MAXILLA								MANDIBLE						
			Faciolingual Diameter		Mesiodistal Diameter		Crown Area			Faciolingual Diameter		Mesiodistal Diameter		Crown Area	
	Side	n	mean	sd	mean	sd	mean	sd	n	mean	sd	mean	sd	mean	sd
i1	R	2	5.25	0.21	6.75	0.07	35.45	1.06	4	4.28	0.93	4.58	0.79	20.05	7.43
	L	2	5.25	0.21	6.70	0.14	35.15	0.64	3	3.87	0.50	4.37	0.81	17.13	5.39
i2	R	2	5.15	0.21	5.80	0.00	29.85	1.20	3	4.70	0.61	5.23	0.72	24.73	5.66
	L	2	4.80	0	5.45	0.21	26.15	1.06	3	4.60	0.56	5.67	1.25	26.53	8.98
c	R	3	5.97	0.65	6.73	0.86	40.53	9.43	4	5.70	0.28	6.03	0.15	34.35	2.01
	L	4	6.20	0.29	6.95	0.19	43.13	3.20	3	5.80	0.20	5.93	0.15	34.43	1.67
m1	R	4	8.75	0.17	7.55	0.58	60.05	8.57	4	7.20	0.27	8.75	0.31	63.08	4.65
	L	4	8.73	0.11	7.53	0.68	65.83	8.14	4	7.15	0.47	8.68	0.33	62.13	5.94
m2	R	4	9.85	0.66	9.53	0.17	93.75	4.72	4	8.73	0.15	10.53	0.29	91.80	1.55
	L	4	10.00	0.39	9.73	0.33	98.28	5.19	4	8.88	0.26	10.55	0.29	93.60	2.67

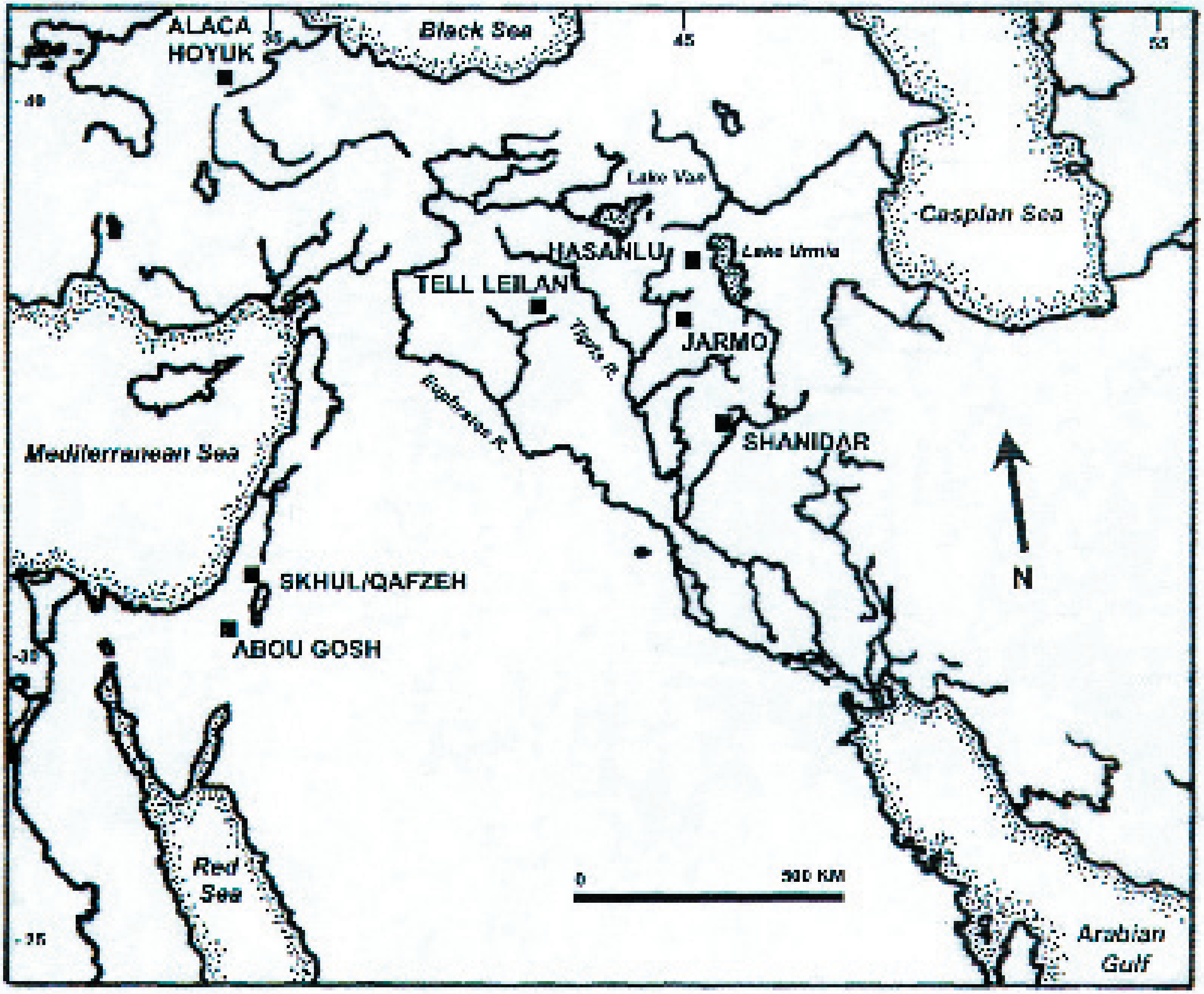

Fig. 1. Map of the Near East showing the sites used in the comparison of total and mean crown areas (Table 3). No sites are shown for the Natufian material, which Dahlberg described only as being from 'Mesolithic Palestine' (Dahlberg 1960:246).

With the exception of the TCA of the modern European sample, which is provided by Brace (1978), all TCA and MCA values were taken from the original MCAs given for each tooth class, or were calculated from published MD and FL crown diameters. In the case of the Neanderthal sample from Shanidar, crown areas for the anterior dentition could not be determined due to extreme occlusal wear (Trinkhaus, 1978), and thus the MCA serves as the primary comparative value. While the Tell Leilan crown diameters were recorded by measuring the maximum mesiodistal breadth for each tooth, it is not explicitly stated in a number of the odontological studies used for this comparison whether this same methodology was followed or whether the breadth between the mesial and distal contact facets of the molar teeth was measured in the manner of Hrdlička (1924) and others. The latter technique may give smaller crown diameters, and hence smaller summed crown areas. Values published elsewhere should thus be considered minimum estimates compared to the Leilan data presented here. This must be taken into consideration when looking at the comparative data, although the size of the difference is likely to be small, on the order of 1 to 2 mm per tooth, based on the personal experience of the authors.

As illustrated in Table 3, the overall trend in permanent tooth size variation is one of gradual reduction over time, beginning in the Middle/Upper Paleolithic with the Skhul/Qafzeh hominids and ending with the modern European population. The sample from Chalcolithic Alaca Höyük in Turkey does not follow this trend, however, having the smallest TCA, smaller even than the modern European sample. Many factors, including method of measurement and the biological affinities of the Alaca Höyük population may account for this difference. Despite this, the overall

TABLE 3. Temporal variation in permanent tooth size among selected Near Eastern archaeological populations[1]

Sample Name	Site Location	Cultural Association	TCA (mm^2)	MCA (mm^2)	Source
Skhul	Israel	Middle Paleolithic	1494	-	Trinkaus, 1978
Qafzeh	Israel	Middle Paleolithic	-	780	Vandermeersch, 1981
Shanidar	Iraq	Upper Paleolithic	-	773	Trinkhaus, 1978
Natufian	Palestine	Mesolithic	1272	722	Dahlberg, 1960
Jarmo	Iraq	Neolithic	1246	679	Dahlberg, 1960
Abou Gosh	Israel	Neolithic	1240	685	Aresnburg *et al*., 1978
Tell Leilan	Syria	Bronze Age	1189	668	this study
Hasanlu	Iran	Iron Age	-	605	Rathbun, 1972
Alaca Höyük	Turkey	Chalcolithic	1161	643	Senyürek, 1952
European	various	Modern	1138	-	Brace, 1978

[1] TCA, Total Crown Area; MCA, Molar Crown Area

trend is in accord with observations made by numerous researchers working in other regions of the world (*e.g*., Brace, 1978; Dahlberg, 1960, 1963; Lukacs and Hemphill, 1991; Sofaer, 1973).

If we examine the values from northern Mesopotamia specifically (*i.e*., Shanidar, Jarmo, and Tell Leilan), it can be seen that a reduction in molar crown area of about 100 mm^2 has taken place in the time span between the Shanidar and Jarmo samples (approx. 55,000 yrs), giving an average MCA reduction rate of almost 0.002 mm^2 per year. Subsequently, the MCA reduction between Jarmo and Tell Leilan is about 10 mm^2, over a span of approximately 4,500 yrs, giving an average MCA reduction that is, also, about 0.002 mm^2 per year. Although additional research is needed, this evidence suggests that the rate of dental reduction does not seem to be linked to subsistence strategy.

Consistent with their fit in the widely recognized trend to dental reduction, the Tell Leilan data support the contention that upper central incisors and the first molars are considered genetically stable. These teeth resist variation in tooth size to a greater extent than do the more distal, *i.e*., later developing, teeth within their respective tooth class (Dahlberg, 1963; Sofaer, 1973) so that the extent of tooth size variation increases distally. The MCA of the upper first molars exhibits a 3.2% difference from Shanidar to Tell Leilan, as compared to a 28.8% change in the upper second molars. Similarly, there is a 2.6% change in lower first molar size from the Shanidar sample to the Tell Leilan sample, and a change of 15.5% in the lower second molars.[3] Further, the change is 2.4% for upper first molars and 11.5% for upper second molars when comparing Tell Leilan and the earlier agricultural sample from Jarmo, and 0% and 4.5% change for lower first and second molars, respectively.

By contrast to the case for permanent teeth, only a few studies have focused on the odontometry of the deciduous dentition (*e.g*., Koenigswald, 1967; Lukacs, 1981; Lukacs *et al*., 1983; Sciulli, 2001; Smith, 1978). Rarely have evolutionary trends in the deciduous dentition been documented, but Smith (1978), Lukacs and Hemphill (1991) and Sciulli (2001) have found that the rate of deciduous tooth size change is relatively stable within the past 5,000 to 10,000 years, roughly half that of permanent teeth (Lukacs and Hemphill, 1991). Table 4 compares the Tell Leilan deciduous TCA to Smith's (1978) data for several Near Eastern populations, from the Epipaleolithic to modern times. It can be seen that, as with the permanent dentition, a distinct reduction trend can be observed over time.

DISCUSSION

Many scholars have debated the mechanisms of dental reduction, but most agree that an overall reduction in tooth crown size should be observed in populations as they move from nomadic hunting and gathering subsistence modes to more sedentary agricultural modes (*e.g*., Dahlberg, 1963; Sofaer, 1973). Indeed, studies have shown that the rate and extent of human dental reduction was at its most profound after the Pleistocene, precisely the time period during which the transition in subsistence modes occurred (Calcagno, 1989; Macchiarelli and Bondioli, 1986; Reddy, 1992).

[3] Crown areas were not available for the Shanidar anterior teeth and thus cannot be compared with values for the Tell Leilan sample

TABLE 4. Temporal variation in deciduous tooth size of selected Near Eastern populations[1]

Cultural Association	n	TCA (mm^2)	n	MCA (mm^2)	Source
Epipaleolithic	139	550	50	333	Smith, 1978
Neolithic	130	504	61	318	Smith, 1978
Chalcolithic	202	459	88	286	Smith, 1978
Middle Bronze Age II	-	-	130	293	Smith, 1978
Bronze Age (Tell Leilan)	35	497	16	319	this study
Iron Age	509	474	-	-	Smith, 1978
Modern	212	454	-	-	Smith, 1978

[1] TCA, Total Crown Area; MCA, Molar Crown Area

Although reduction in the size of the dentition occurred during the Pleistocene, this reduction may be related to an overall reduction in body size or robusticity, especially in the masticatory apparatus and facial skeleton in general (Macchiarelli and Bondioli, 1986; Brace et al., 1991). Alternatively, selective pressures that favored larger or smaller teeth, depending on specific environmental conditions affecting dental health, may act as the primary mechanism of reduction (Calcagno, 1989; Calcagno and Gibson, 1991). Such conditions may have included dietary toughness and/or abrasiveness. Early cultural advancements such as food preparation techniques (e.g., the use of fire to cook raw plant and animal foods), pottery, increasingly sophisticated tools, and changes in diet also may have played a role in selecting for smaller tooth sizes.

Given the paucity of odontological data for this area, however, it is not within the scope of this paper to determine the exact mechanisms of dental reduction for the region of Northern Mesopotamia. Presently, there are no sources of modern Near Eastern odontometric studies suitable for comparative purposes. Rosensweig and Zilberman's (1969) odontometric analysis of modern Bedouin in Israel did not include the third molars. Thus, the TCA for a modern European population (Brace, 1978) is included in Table 3 as an illustration of the extent of dental reduction since the Middle Paleolithic. Studies of modern human populations have shown that the smallest tooth crown dimensions today are observable in Europeans and certain Asian populations (Dahlberg, 1963; Lukacs, 1985). Some researchers have argued that this is because these regions were some of the earliest sites of sedentary agricultural development, and consequently have had the longest amount of time for dental reduction to occur (Brace, 1978; Reddy, 1992). Because the region of Mesopotamia is also one of the earliest sites of agricultural development, the same small tooth dimensions should be expected for modern Near Eastern populations. However, in all cases, extenuating factors such as genetic makeup, the migration of peoples and genetic drift will also play a role, the extent of which may be hard to determine at this time. What needs further investigation is that the rate of dental reduction appears to have remained constant through a transition from Upper Paleolithic hunting-foraging through the origins of food production and into the metal ages (data in Table 3). This is, in fact, contrary to predictions of tooth size according to modes of subsistence, and may lend credence to explanations based on overall decreases in skeletal robusticity, which were more pronounced between the Upper Paleolithic and the Neolithic than between the Neolithic and the metal Ages.

CONCLUSIONS

Results reported here of the metric analysis of the permanent and deciduous dentition of the northern Mesopotamian Bronze Age site of Tell Leilan, when compared with odontometric data from varying periods within the Near East, are consistent with the pattern of hominid dental size reduction observed worldwide since the Middle Paleolithic. The total crown areas (TCA) for the Tell Leilan permanent and deciduous dental samples, 1189 mm^2 and 497 mm^2, respectively, place this archaeological population at the smaller end of the crown area scale for the Near East; smaller in size than nearby Paleolithic and Neolithic populations, and slightly larger than more recent populations and the modern samples. The rate of reduction in hominid dentition has varied both spatially and temporally over the course of human evolution (e.g., Calcagno, 1989; Macchiarelli and Bondioli, 1986; Reddy, 1992), and factors such as genetic drift and the blending of geographically diverse populations over time often obscure or complicate our understanding of human dental reduction, especially in the post-Paleolithic. It is hoped that larger dental samples from a wider variety of sites in ancient Mesopotamia will eventually allow for a more detailed documentation of metric dental trends in this region and time period of the Near East.

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Examination of the Rare Labial Talon Cusp on Human Anterior Teeth

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ABSTRACT The labial talon cusp, a triangular ridge of enamel near the midline of anterior teeth, has been observed in archaeological remains and modern dental patients. The purpose of our report is to describe new cases in order to provide better estimates of its frequency, symmetry, teeth involved, and geographic occurrence. This research was initiated after a labial talon cusp was found in a Caddo cranium curated in the Texas Archaeological Research Lab at the University of Texas at Austin. Subsequently, we identified additional examples resulting in the total of eight new cases presented here. Five cases were identified in the Native American Pima dental casts from the A. A. Dahlberg collection at Arizona State University. Two of the Pima cases were found in a systematic analysis of 1,835 dental casts for a population frequency of 0.11%. Additional cases were identified in Ainu and Anasazi skeletal material. Including these new finds, 15 cases of labial talon cusp are now known including Native Americans, African Americans, Japanese, Australians, and Europeans. Six cases are maxillary and nine are mandibular. Known maxillary cases are unilateral, while 55.6% of the mandibular cases are bilateral. All anterior teeth appear to be affected, but there is no recorded instance of an affected mandibular canine. *Dental Anthropology* 2003;16(3):81-83.

Recently, several authors have reported on the presence of a cusp-like structure on the labial aspect of anterior human teeth (Abbott, 1998; Jowharji et al., 1992; McNamara, 1997; McNamara et al., 1997; Schulze, 1987; Tomonori and Ogouchi, 1991; Turner, 1998). This feature is described as a triangular ridge of enamel, or a style near the midline of the tooth, located on the labial surface. The apex of this accessory structure terminates near the occlusal edge. Radiographs have shown this style to be made up of enamel and dentine, with sporadic pulp involvement (Abbott, 1998; Jowharji et al., 1992; McNamara, 1997; Tomonori and Ogouchi, 1991). Previous studies have referred to this feature as a facial talon cusp, labial talon cusp, and, simply, talon cusp (Abbott, 1998; Jowharji et al., 1992; McNamara, 1997). Since the *talon cusp* is more frequently used to refer to an accessory structure on the lingual aspect of the upper teeth, we suggest the use of the term "labial talon cusp."

Seven cases of labial talon cusp have been previously reported in the literature. Three cases were modern European; mandibular central incisors were affected in two individuals and a maxillary canine was affected in the remaining individual (McNamara, 1997; McNamara et al., 1997; Schulze, 1987). One case was a modern Japanese with a mandibular central incisor involved (Tomonori and Ogouchi, 1991). A labial talon cusp on the maxillary central incisor has been identified in a modern African American (Jowharji et al., 1992). Abbott (1998) found a modern Australian case with an affected maxillary central incisor. Lastly, Turner (1998) reported a labial talon cusp found on the maxillary lateral incisor from an archaeological Native American Anasazi.

RESEARCH AND RESULTS

New Cases

Eight new cases of labial talon cusp have been recorded by the authors. Bilateral labial talon cusps were identified archaeologically in the mandibular central incisors of an Ainu (Japan) (Fig. 1) and a Caddo (Texas) (Fig. 2). Five cases affecting the mandibular central incisors were found among dental casts of living Native American Pima; three were bilateral (Fig. 3) and two unilateral. One unilateral case had the left central incisor rotated 180°, with the labial talon cusp facing the inside of the mouth. One archaeological Native American Anasazi was found to have a labial talon cusp on a maxillary incisiform supernumerary tooth situated between the central incisors, a mesiodens (Fig. 4).

There are few data on the frequency of this rare anomaly. Our original specimen was encountered during an analysis of 132 Native American Caddoan crania, from the collections at the Texas Archaeological Research Laboratory, University of Texas at Austin. All permanent teeth were examined. This yielded a labial talon cusp frequency of 0.76% for the Caddo. To determine the frequency of labial talon cusps in a large sample of Native Americans we subsequently examined a series of 835 female and 1,000 male dental casts from the Arizona State University A. A. Dahlberg Native American Pima dental casts. This analysis, limited to the mandibular and maxillary permanent incisors,

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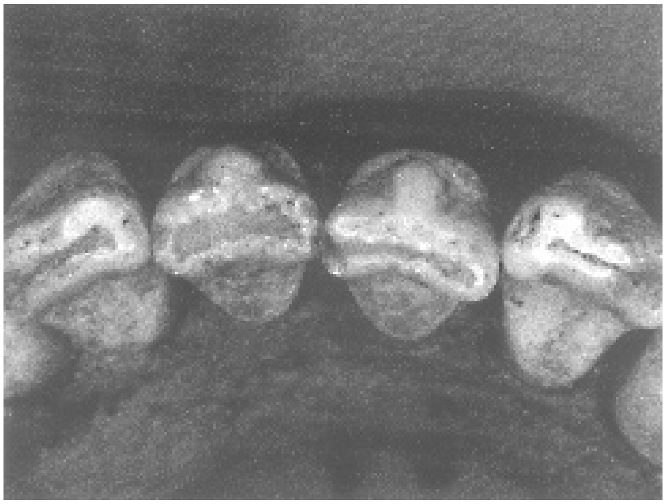

Fig. 1. Japanese (Ainu). Bilateral expression on mandibular central incisors.

Fig. 2. Native American (Caddo). Bilateral expression on mandibular central incisors.

yielded two cases for a population frequency of 0.11%. These data indicate the labial talon cusp is a rare trait with a population frequency of less than 1%.

Casts of the relatives of all five Pima individuals were examined since no familial case is known to date. Three parents and 19 siblings were examined but no additional labial talon cusp occurred. There is no evidence to suggest the five affected Pima were closely related to each other.

SUMMARY OF PRESENTLY KNOWN CASES

At the present time, a total of 15 individuals have been observed with at least one labial talon cusp (Table 1). All cases were found in the permanent dentition. Six cases of labial talon cusp were found on the maxillary teeth; all were female and unilateral. Three cases involved a maxillary central incisor while one case appeared on a lateral incisor. Labial talon cusps were also identified on a maxillary canine and an incisiform supernumerary tooth. There is some uncertainty if the supernumerary tooth exhibits a true talon cusp or some other abnormal morphology.

Nine cases of labial talon cusp involved the mandibular central incisors alone. Eight individuals of the nine were of known sex—two female and six male. Expression on the mandibular central incisor was bilateral in five out of nine cases (55.6%). Although only 15 cases are known, females appear to express the trait more often in the maxillary teeth, while males account for most cases in the mandibular teeth. There are no cases involving maxillary and mandibular teeth in the same individual. One known case exhibits a labial and a lingual talon cusp on the same tooth (Abbott, 1998).

TABLE 1. Known Cases of labial talon cusp

Group	Sex	Teeth	Source
1. Japanese	F	Max. left I1	Tomonori *et al*., 1991
2. African American	F	Max. right I1	Jowharji *et al*., 1992
3. Irish	F	Max. right C	McNamara *et al*., 1997
4. Australian	F	Max. left I1	Abbott, 1998
5. Native American (Anasazi)	F	Max. left 12	Turner, 1998
6. Native American (Anasazi)	F	Max. supernumary I	This study
7. German	?	Mand. right I1	Schulze, 1987
8. Irish	M	Mand. left I1	McNamara, 1997
9. Native American (Pima)	F	Mand. left I1, right I1	This study
10. Native American (Pima)	F	Mand. left I1	This study
11. Native American (Pima)	M	Mand. left I1, right Il	This study
12. Native American (Pima)	M	Mand. left I1 and right I1	This study
13. Native American (Pima)	M	Mand. left I1	This study
14. Native American (Caddo)	M	Mand. left I1 and right I1	This study
15. Japanese (Ainu)	M	Mand. left I1 and right I1	This study

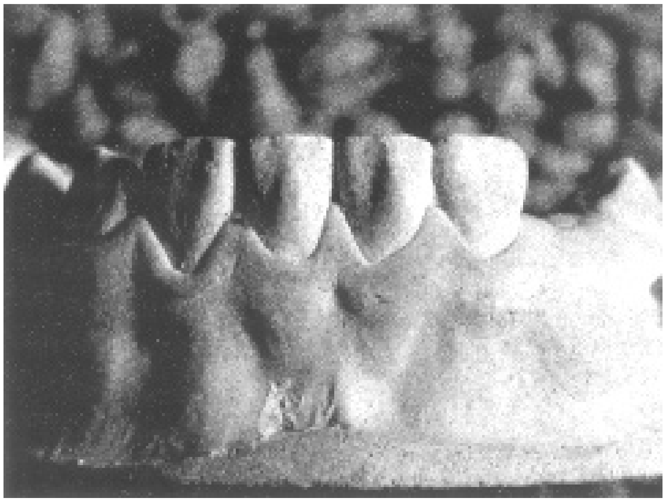

Fig. 3. Native American (Pima). Bilateral expression on mandibular central incisors.

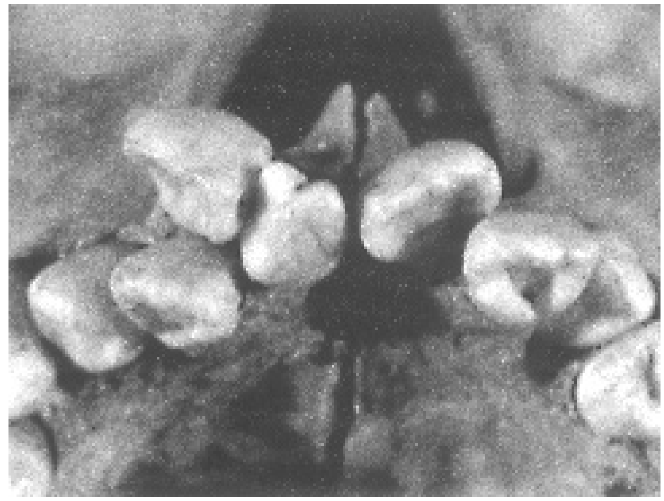

Fig. 4. Native American (Anasazi). Maxillary incisiform supernumerary tooth with labial talon cusp.

CONCLUSIONS

This study presents eight new cases of the rare labial talon cusp and the first estimates of population frequencies. The labial talon cusp is rare and found in less than one percent of the population. Labial talon cusps have been found on all maxillary and mandibular anterior teeth, except mandibular canines. To date, little evidence indicates a direct relationship between the labial talon cusp described here and the more common lingual talon cusp. Possible uses for this trait may be in the research of dental development (Jowharji et al., 1998), dental evolution (Turner, 1998), or genetic syndromes (Tomonori and Ogouchi, 1991). Hopefully future research will enable us to better understand the etiology and genetic basis of this trait, as well as any possible correlation that may relate to other morphological features of the human dentition.

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Where's the Variation? Variance Components in Tooth Sizes of the Permanent Dentition

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ABSTRACT Studies have shown that there are only a few canonical axes of tooth size variation in the permanent dentition. Despite the numerous measurements that might be taken (*e.g.*, crown length and breadth of 32 teeth = 64 variables), most of the canonical structure is explained by 3 or 4 overarching axes of variation. This study used maximum likelihood components of variance analysis to determine where the major sources of statistical variation are among the crown dimensions in the permanent dentition. Mesiodistal and buccolingual crown dimensions were measured on all permanent teeth (excluding M3s and averaging sides) in 100 American whites and 100 American blacks, evenly divided by sex. The SAS program *varcomp* estimated the sources of variation across 7 aspects of the dentition, namely race, sex, arcade, tooth (incisor, canine, premolar, molar), position (mesial, distal), dimension (MD, BL), and a residual term. Most variation is shared; residual variance was just 21.8% of the total. Considering the six components of shared variance, the greatest (82.8%) was due to tooth type (I, C, P, M). In contrast, only 4.9% was attributable to the black-white race difference, which confirms results of other biological data that the preponderance of variation is within groups, not among them. More striking is the lack of variation between males and females (1.2%)—confirming the insensitivity of tooth crown dimensions for forensic purposes. Very little shared variance (0.6%) was due to tooth position, indicating that the mesial "pole" tooth that is metrically and morphologically more stable does not possess much more informational content statistically. Whether the tooth was maxillary or mandibular accounted for 6.9%. In a practical sense, the large variance due to tooth type implies that dental anthropologists commonly will want to include variables from all tooth types (I, C, P, M) rather than multiple measurements within a tooth type, since tooth type is *the* canonical axis of variation. *Dental Anthropology* 2003;16(3):84-94.

If one measures the conventional mesiodistal and buccolingual crown diameters of the 32 permanent teeth in the human dentition, there are 64 variables, which is comparable to an extensive battery of craniometrics or anthropometrics (*e.g.*, Davenport, 1927; Martin, 1928). One might suppose that there is a lot of statistical information—several axes of variation—in the odontometrics based on tooth types, side, arcade, a tooth's position in its morphogenetic field, sex, race, and so on. However, the morphological and statistical redundancy among tooth types has long been recognized, and this redundancy sharply diminishes the information content of batteries of crown dimensions. Bateson (1894) included teeth in his anatomic examples of meristic series that included phalanges, vertebrae, and ribs. This phenomenon of multiple analogous skeletodental units that develop clinally along a growth axis also is termed *polyisomerism* (Gregory, 1934). The supposition is that the shared morphologies are controlled by common control mechanisms (genes, gene products), but verification has only recently been provided (*e.g.*, Yamaguchi, 1997; Green, 2002). Weiss (1990), Jernvall (2000; Jernvall and Jung, 2000; Jernvall and Thesleff, 2000), and others suggest that polyisomerism is a conservative, efficient mechanism for increasing (or, occasionally, decreasing) the anatomic units, which is more obvious phylogenetically, but occurs ontogenetically as well. The "several" canonical axes of variation expected from a battery of tooth dimensions do not actually occur because tooth crown dimensions are invariably positively intercorrelated (*e.g.*, Moorrees and Reed, 1964; Potter *et al*., 1968; Henderson, 1975; Townsend, 1976; Harris and Bailit, 1988).

Genetic covariance among continuous-scale variates like crown dimensions arises from pleiotropic effects of the contributing genes (*e.g.*, Falconer, 1989). Indeed, the principal theme of Butler's seminal studies of morphogenetic fields (1939, 1956, 2001) is the developmental dependencies (covariance) of tooth morphologies and dimensions of teeth within the three major fields in mammals, namely incisors, canines, and postcanine tooth types. The consequences for the dental anthropologist are that much of the informational content of many tooth crown dimensions are statistically redundant. Measuring more teeth or measuring more dimensions of the same teeth does not proportionately increase

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the researcher's ability to discriminate between sexes, or populations, or races, or species. Falk and Corruccini (1982) have shown this quite simply: the discriminatory power among groups was much better using craniometric variables (with less covariance among traits; Solow, 1966) than an equivalent battery of tooth crown dimensions.

MATERIALS AND METHODS

The data analyzed here consist of maximum mesiodistal (MD) and buccolingual (BL) tooth crown dimensions of all 14 permanent tooth types, omitting M3s. Measurements were made on the full-mouth dental casts of 100 American whites and 100 American blacks using electronic-readout sliding calipers with the beaks machined to fit well into the embrasures between teeth. Measurement technique followed that described by Selmer-Olson (1949). There was an equal number of males and females in each race, and the subjects were contemporary American adolescents with all 28 teeth fully erupted without any restorations that would affect the measurements. Teeth on just one side of the mouth were measured (either left or right, on an individual basis), but numerous studies have shown that the variance attributable to side is meager and due to just bilateral asymmetry plus technical error and may safely be ignored without biasing the other effects (*e.g.*, Lundström, 1948; Potter and Nance, 1976).

Statistical analysis

It is implausible from what is known about odontometrics (*e.g.*, Kieser, 1990; Hillson, 1996) to suppose that either genetic or environmental variation in tooth size is distributed across the dentition in even a vaguely uniform manner. Instead, some of the axes of variation will account for appreciably more than other sources of variation. Six axes of variation were estimated in the present study. Variation was compared by (1) race, (2) sex, (3) arcade (maxilla or mandible), (4) tooth type (incisors, canines, premolars, and molars), (5) dimension (mesiodistal versus buccolingual crown diameters), and (6) position (the mesial or distal tooth within a morphogenetic field).

To find out how the variance in tooth size is apportioned across these six axes, model II, maximum-likelihood estimates of variance components were estimated (Hartley *et al.*, 1978) using the SAS procedure *varcomp* (SAS, 1989).

Two "races" were contrasted, American blacks and whites, but the perspective is to view these as random samples from the "universe" of possible races (*e.g.*, Coon, 1965). Similarly, any number of crown dimensions could be measured on a tooth (cf. Corruccini, 1977, 1978; Black, 1979; FitzGerald and Hillson, 2002), the conventional two assessed here (*i.e.*, the standard MD and BL dimensions) are best viewed as a sample of two picked from a population of dimensional possibilities.

RESULTS AND DISCUSSION

Multivariate analysis

Most of the total variance for odontometrics is shared (common) rather than unique variance. This has long been recognized (*e.g.*, Garn *et al.*, 1965, 1968; Moorrees and Reed, 1964) insofar as all MD and BL crown dimensions are positively intercorrelated with one another throughout the dentition. This is true for the present data set (Table 1) where every one of the 378 pairwise comparisons is positively and significantly correlated at $P < 0.001$ ($n = 200$ for each comparison). This means that "size" is a pervasive controlling factor throughout the dentition. It also means that (1) tooth size can be predicted with some accuracy from other tooth sizes (*e.g.*, Moyers, 1988; Tanaka and Johnston, 1974) but that (2) since all dimensions are intercorrelated, they all tend to estimate the same thing (namely "overall size") rather than carrying unique, nonredundant information. Developmentally, these statistical intercorrelations appear to reflect the communalities of a few rather than many axes of ontogenetic control (Weiss, 1990; Salazar-Ciudad and Jernvall, 2002).

Statistical redundancy also has been illustrated in the several studies of human tooth size using factor analysis (*e.g.*, Potter *et al.*, 1968; Harris and Bailit, 1988). For the present data, there are just three orthogonal axes of shared variation among the 28 crown dimensions, with "overall size" accounting for most (83%) of this (Fig. 1). The other two axes of variation are (1) BL breadths of the anterior teeth contrasted with MD lengths of the cheek teeth (premolars and molars), accounting for 10% of the shared variation, and (2) MD lengths of the incisors contrasted with BL breadths of the posterior teeth (canines, premolars and molars) accounting for 7%. Collectively, these three axes of shared variation (*i.e.*, variation not unique to a single crown dimension) is 73% of the total variation.

PCA has been performed across a broad range of human samples, showing concordant results and, thus, the nature of the covariance matrices probably is essentially independent of the population under study. It is obvious that these three canonical axes of metric control of the dentition are far fewer than the 28 variables measured for the dentition, and this "reduction" is due to statistical (and developmental) redundancy among crown sizes.

Variance components

Results from the SAS program *varcomp* disclosed that, taking total variance as 100%, the shared variance accounted for by the six variables in the model was 79.2% while the residual variance, unique to individual measurements accounted for the other 21.8% (Fig. 2). This is about a four-to-one ratio of explained to residual variances, suggesting that the six factors listed above do,

TABLE 1. Partial correlation coefficients above the main diagonal, covariances on the diagonal, and full correlation coefficients below the diagonal

	Mesiodistal														Buccolingual													
	Maxilla							Mandible							Maxilla							Mandible						
	I1	I2	C	P1	P2	M1	M2	I1	I2	C	P1	P2	M1	M2	I1	I2	C	P1	P2	M1	M2	I1	I2	C	P1	P2	M1	M2
UI1 MD	**.806**	.339	.099	-.010	.012	.129	.073	.413	.184	.012	-.110	-.128	.065	-.056	-.071	.023	-.138	-.017	.207	.002	.033	-.147	.128	.144	-.103	.032	.032	.004
UI2 MD	.737	**.690**	-.026	.115	.002	-.176	-.020	.029	.072	.173	.071	.022	.026	.009	.094	.258	-.002	-.030	.029	-.081	-.104	.112	-.143	-.098	.041	-.109	.062	.070
UC MD	.662	.582	**.722**	.143	-.071	-.027	.089	.071	-.049	.381	-.025	.097	.135	-.093	.069	-.105	.232	.061	-.067	.095	-.025	.056	-.038	.020	-.075	-.045	.027	-.086
UP1 MD	.673	.662	.703	**.884**	.407	.084	.054	-.058	.141	-.012	.475	-.019	-.071	-.016	-.034	-.026	.017	.227	-.041	-.058	-.045	-.091	.103	.018	-.040	-.055	-.123	.188
UP2 MD	.564	.529	.584	.816	**.748**	.061	.032	-.027	-.004	-.043	-.108	.291	-.014	.032	.095	-.055	.026	-.081	.185	-.022	.089	.021	-.006	-.043	-.043	.056	.019	-.121
UM1 MD	.637	.491	.617	.697	.659	**.788**	.418	.121	-.021	.020	-.125	.197	.318	.020	-.029	.231	-.135	-.075	.007	.189	-.111	-.101	-.021	.034	-.019	-.029	.079	-.069
UM2 MD	.578	.493	.620	.723	.671	.771	**.768**	-.136	-.038	-.077	.094	-.084	-.031	.264	.047	-.092	.111	.030	.023	-.187	.213	.173	-.072	-.058	.057	.039	-.014	-.018
LI1 MD	.814	.663	.610	.635	.517	.572	.502	**.787**	.408	-.045	.124	-.016	-.077	.044	.083	-.122	.095	-.036	-.012	.008	.018	.138	.036	-.187	.046	.037	-.132	.082
LI2 MD	.777	.683	.620	.703	.562	.591	.532	.823	**.786**	.192	.045	.043	-.041	.103	-.007	-.013	-.072	.023	-.216	.051	-.029	.034	.059	-.042	.045	.035	.067	-.064
LC MD	.705	.663	.787	.739	.618	.635	.617	.644	.708	**.783**	.038	.042	.103	.041	-.073	-.018	-.027	-.007	.043	.008	.098	-.083	.033	.221	.091	.100	-.057	-.014
LP1 MD	.640	.646	.667	.891	.745	.687	.715	.633	.694	.734	**.866**	.300	.064	.173	-.067	.133	-.115	.013	.061	.018	.039	-.082	.006	.008	.105	-.014	.032	-.144
LP2 MD	.586	.556	.659	.806	.784	.728	.683	.566	.627	.706	.834	**.811**	.087	.029	-.073	-.054	-.038	.005	.057	-.032	-.012	.011	.079	-.046	.048	.165	.076	-.054
LM1 MD	.618	.548	.669	.695	.626	.794	.707	.553	.598	.687	.721	.730	**.790**	.351	.065	-.006	.043	.120	-.096	.038	-.098	-.010	-.045	-.171	.046	-.086	.211	.000
LM2 MD	.619	.564	.619	.744	.664	.730	.783	.599	.642	.681	.771	.722	.790	**.808**	-.130	.050	.041	-.096	.027	-.079	.228	.081	.004	-.005	-.084	-.032	-.112	.228
UI1 BL	.422	.449	.468	.406	.378	.361	.393	.420	.379	.420	.360	.328	.370	.354	**.604**	.325	.148	.063	-.042	.169	.044	.093	.174	-.035	.016	-.027	-.077	-.038
UI2 BL	.499	.577	.490	.529	.448	.503	.490	.433	.447	.517	.524	.453	.478	.497	.663	**.654**	.213	.132	-.064	.021	.007	.170	-.019	.092	.012	-.013	-.068	-.102
UC BL	.451	.434	.607	.527	.481	.420	.534	.415	.381	.561	.473	.466	.462	.508	.591	.604	**.675**	-.038	.152	-.059	.094	-.102	.133	.263	-.051	.125	.024	.072
UP1 BL	.644	.592	.687	.810	.710	.646	.694	.566	.592	.730	.778	.746	.686	.683	.494	.583	.623	**.867**	.494	-.008	.155	-.123	.093	-.049	.192	.010	.046	.033
UP2 BL	.639	.565	.642	.752	.723	.621	.677	.538	.523	.700	.731	.729	.623	.654	.455	.538	.639	.884	**.855**	.099	-.016	.129	-.124	.065	.122	.225	-.040	-.023
UM1 BL	.602	.482	.638	.607	.552	.643	.581	.552	.559	.652	.599	.607	.657	.628	.530	.519	.568	.710	.686	**.792**	.412	.057	.011	-.003	.019	-.021	.309	.139
UM2 BL	.597	.497	.638	.689	.633	.631	.714	.549	.558	.680	.680	.649	.657	.746	.487	.521	.617	.764	.727	.802	**.800**	-.026	-.049	.000	.009	-.085	-.040	.189
LI1 BL	.475	.466	.480	.434	.392	.378	.461	.494	.461	.473	.406	.395	.380	.469	.602	.589	.558	.480	.497	.530	.505	**.705**	.510	.194	-.056	.014	.007	.046
LI2 BL	.591	.513	.583	.589	.500	.469	.503	.580	.576	.603	.543	.524	.473	.531	.629	.599	.636	.620	.584	.606	.585	.787	**.770**	.185	.104	-.065	.036	.035
LC BL	.408	.348	.470	.396	.329	.301	.361	.302	.318	.515	.354	.332	.278	.346	.479	.519	.632	.482	.508	.470	.466	.604	.650	**.608**	.133	-.082	.048	.003
LP1 BL	.592	.554	.616	.716	.633	.592	.630	.554	.581	.710	.723	.707	.622	.627	.450	.524	.578	.815	.795	.668	.690	.487	.618	.510	**.764**	.263	.005	.083
LP2 BL	.538	.449	.550	.630	.613	.541	.572	.496	.505	.631	.628	.680	.548	.563	.340	.403	.540	.721	.761	.599	.608	.398	.491	.391	.749	**.689**	.129	.123
LM1 BL	.559	.467	.584	.578	.531	.625	.570	.477	.521	.609	.581	.626	.687	.609	.374	.412	.509	.669	.639	.775	.681	.442	.531	.408	.648	.633	**.746**	.380
LM2 BL	.595	.516	.584	.647	.544	.580	.613	.556	.555	.636	.608	.601	.643	.698	.416	.442	.576	.708	.678	.761	.767	.508	.590	.448	.686	.648	.783	**.775**

collectively, account for most of the variability in this data set in the statistical sense. Variance components of the six factors tested here are expressed as percentages of the explained variance (Table 2).

Caveat

Partitioning total phenotypic variance into the relative fractions due to the six sources (listed above) is done to disclose differences in the relative contributions of these contributors to anatomic variation. So, for example, variations among the four tooth types (58.8% of total) is found to be enormously greater than variations between the MD and BL crown diameters at 2.5% (*i.e.*, between the two conventional axes used to reflect size

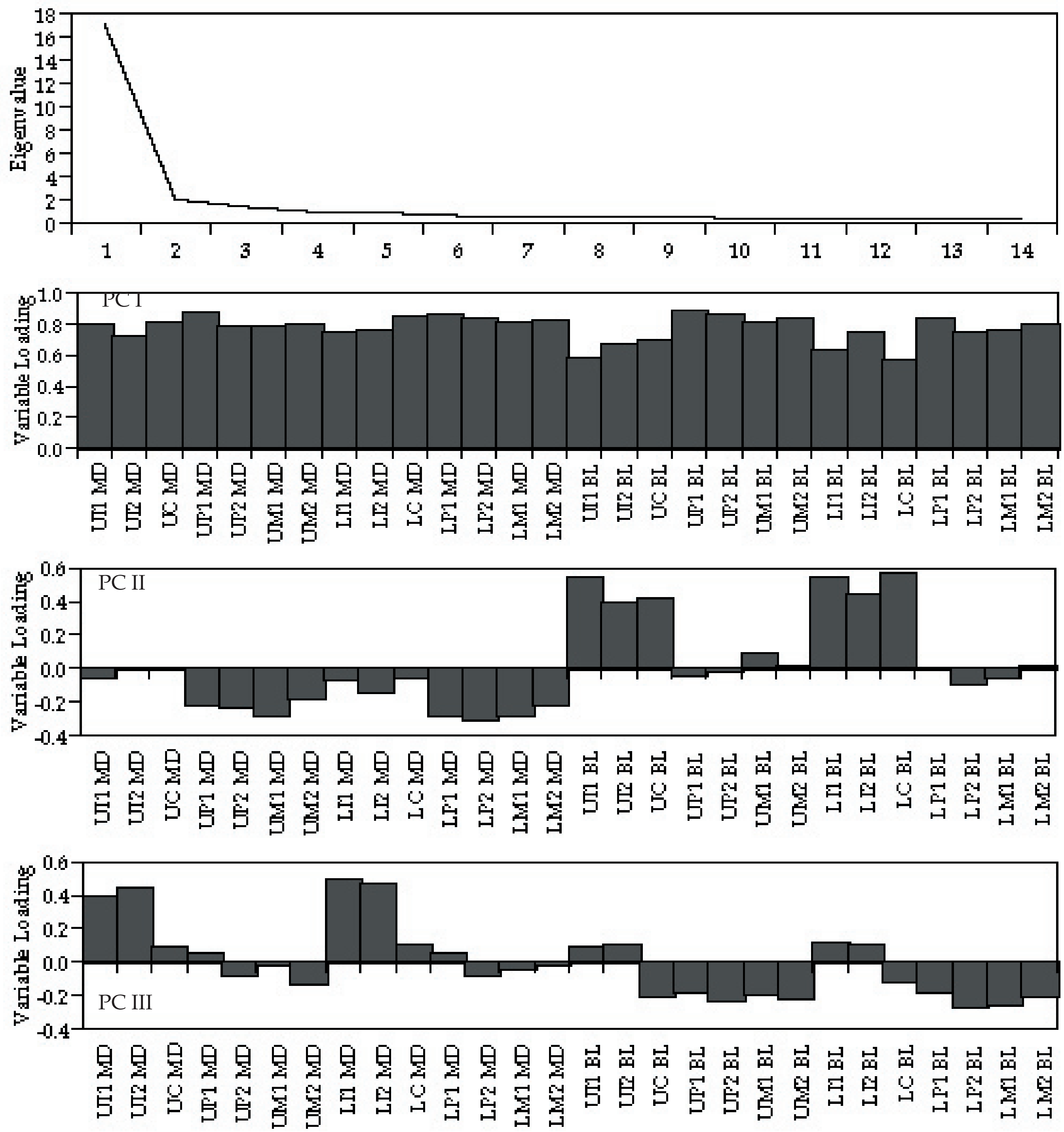

Fig. 1. Results of principal components analysis on the 200 cases in the present study (28 crown dimensions). **Top**: Distribution of eigenvalues showing how most of the variation is in the first canonical component and how quickly the subsequent values descend, so that just the first three are larger than 1.0. The other three panels are graphs of the variables' weights on each of the three principal components.

variation). Whether large or small, these components do not address whether there are statistically significant differences between groups within one of these six canonical dimensions. For example, the smallest source of variation in the present analysis is "position"—whether a tooth is the mesial, stable tooth or the distal, variable tooth within a morphogenetic field (I, P, M). Even though position only accounts for 0.4% of the total variance, there still are highly significant statistical differences in mean size and in variance between mesial and distal teeth within a field (Kieser, 1990). Consequently, these two issues (source of variation *versus* statistical significance) are unrelated issues.

Tooth type

By far, the largest variance component (82.8%) is tooth type, namely whether the tooth is an incisor, canine, premolar, or molar (Fig. 3). This finding has an intuitive appeal because heterodonty—the segmentation of the dentition into functionally specialized tooth types (incisors for nipping, canines for piercing, premolars for trituration, and molars for crushing)—is the fundamental arrangement of the primate dentition (Todd, 1918; Butler 1939, 1956; Swindler, 2002). The other anatomic effects in the present analysis simply involve duplication within the fields: duplication across the upper and lower arch producing structurally similar antagonists; duplication of a distal tooth creating the short meristic series that Weiss (1990), Jernvall (2000; Jernvall and Jung 2000), and others point out is an efficient method of increasing the number of structures, essentially by duplicating existing ones. The other sort of duplication (not included here) is tied to the ontogeny of bilateral symmetry, where left and right paired structures develop, apparently using the same genetic information, symmetrically across the midline. It would seem, then, that the four morphogenetic fields (one for each tooth type) constitute the basic organizing theme—with most of the variation among fields—and that, within fields, teeth enumerated front-to-back (the "pole" and the "variable" tooth; Dahlberg, 1945, 1951), side-to-side (bilateral symmetry), and craniocaudally (creating analogous tooth morphologies in the two jaws) consume *comparatively* little variation. In a practical sense, this large variance due to tooth type implies that dental anthropologists commonly will want to include variables from all tooth types (I, C, P, M) rather than multiple measurements within a tooth type, since tooth type is *the* canonical axis of variation.

TABLE 2. Estimates of the proportion of variance for each of the 7 parameters in the model

Source	Estimate	Percentage
Tooth Type	2.47247	58.76
Arcade	0.20484	4.87
Race	0.14707	3.49
Dimension	0.10735	2.55
Sex	0.03633	0.86
Position	0.01656	0.39
Residual	0.83461	19.84
Total		100.00

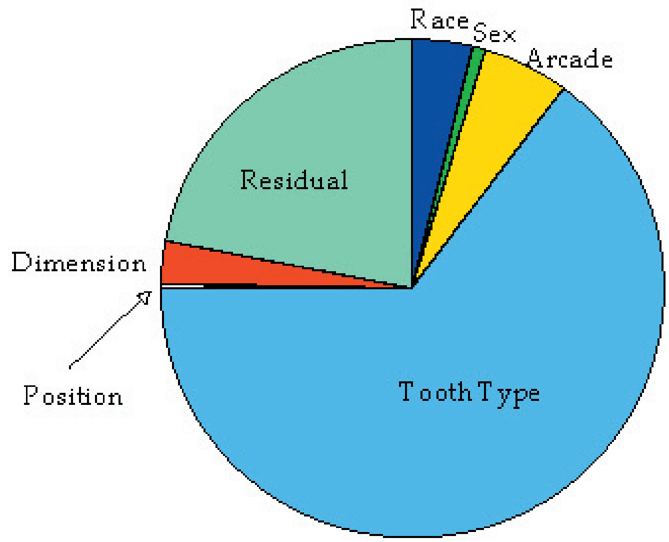

Fig. 2. Pie chart showing the apportionment of tooth size variation based on the six variables in the model (see text for details).

Arcade

While it is a distant second in terms of absolute variance, arcade (Fig. 4) counts for the next-largest component of variance (6.9%), which is in concert with the results of factor analysis of dental metrics showing that, aside from an overall size effect, most factors or principal components (*i.e.*, intercorrelated multivariable dimensions of teeth) typically are arcade-specific (*e.g.*, Potter *et al.*, 1968; Brown and Townsend, 1979). Perhaps this has been shown most clearly by Potter *et al.* (1976) who characterized the few axes of genetic variation in the dentition. One genetic factor was bilateral sym-

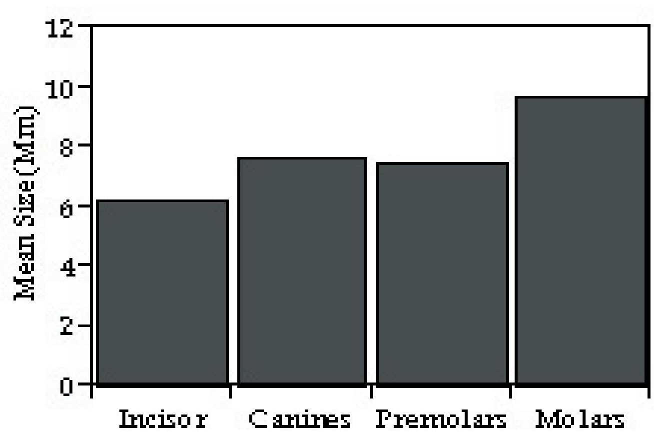

Fig. 3. Graph of mean tooth size by tooth type.

metry; every genetic factor identified for a dimension on one side included the antimeric dimension on the other. Secondly, Potter disclosed a buccolingual crown size factor that extended throughout the maxillary (but not the mandibular) teeth. Thirdly, a genetic factor influenced both MD and BL dimensions of the mandibular anterior teeth. It is noteworthy that these genetic factors control *regions* of the dentition, not specific teeth. Recent computer modeling (Salazar-Ciudad and Jernvall, 2002) shows comparable results, namely that controlling just a few parameters can account for both the ontogenetic and phylogenetic variations within and among tooth types, both metrically and morphologically.

In the present study, Figure 4 displays the arcade differences graphed across the 14 tooth crown dimensions.

Race

The estimate of variance for "race" in this study might be criticized because only two groups were included and because American blacks and whites have experienced several generations of low level gene flow, primarily from whites to blacks (literature reviewed in Pollitzer, 1999).

On the other hand, Subsaharan Africans and American whites are at either end of the contemporary spectrum of human tooth sizes (Harris and Rathbun, 1991), except of course for the megadont native Australians (*e.g.*, Smith *et al*., 1981). Odontometric studies of American blacks and whites routinely find that blacks possess significantly larger teeth (Richardson and Malhotra, 1975; Macko *et al*., 1979; Vaughan and Harris, 1992). In the future, it may be informative to increase the mix of ethnic samples in this assessment of the sources of tooth size variation.

The critical issue, however, is recognition of the small component of variance attributable to the black-white difference, estimated here at 3.5% (Fig. 5). The minor contribution of "race" is no longer surprising (Lewontin, 1972), but these data are confirmatory, using quite a different tissue system, that races have been defined historically using very superficial criteria, whereas the great preponderance of variation is among individuals within groups, not among them.

Dimension

Dimension of the tooth crown—whether the crown is measured mesiodistally or buccolingually—accounted for 3.6% of the total variance. This is interesting because it shows that these geometrically orthogonal axes of a

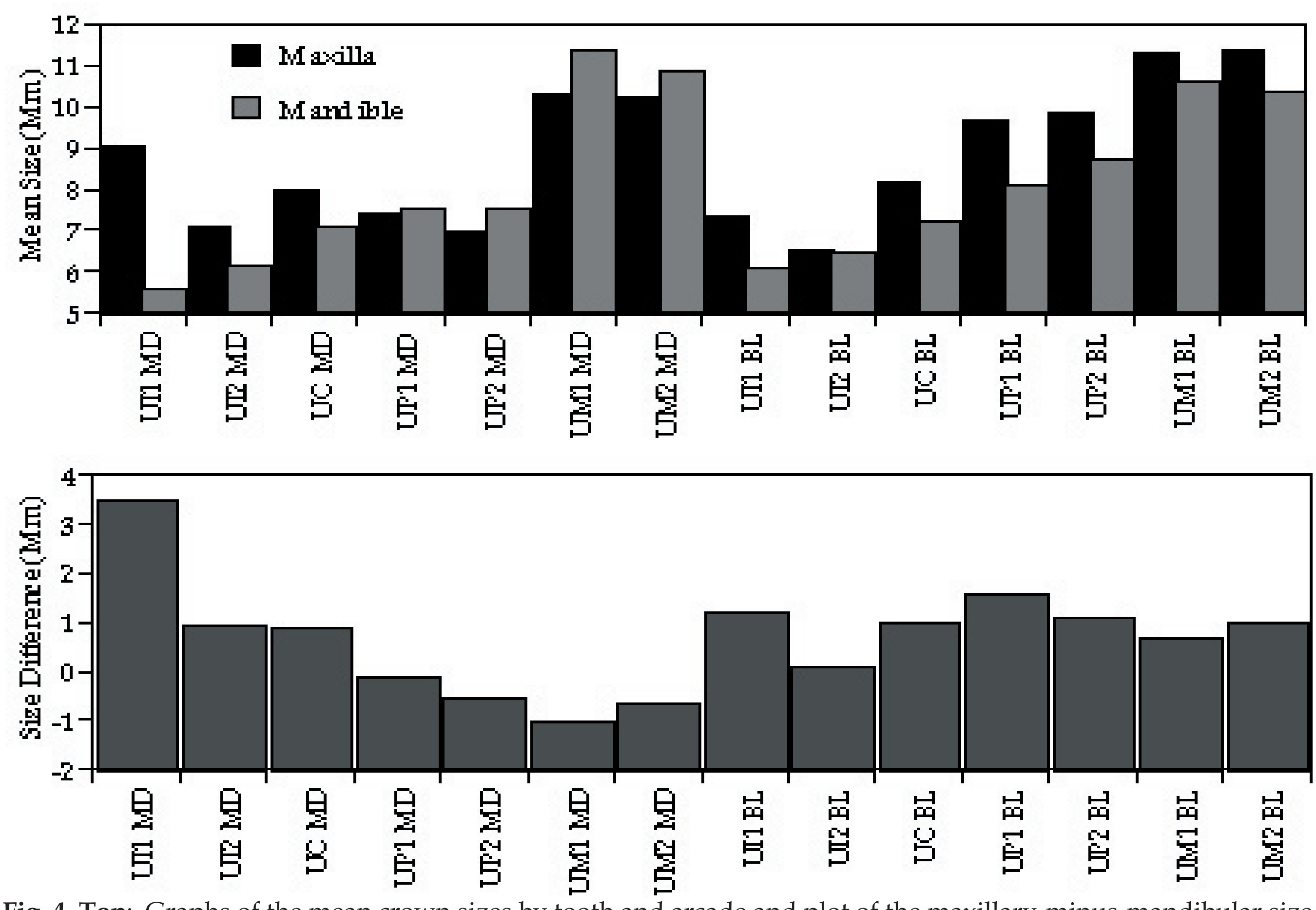

Fig. 4. **Top**: Graphs of the mean crown sizes by tooth and arcade and plot of the maxillary-minus-mandibular size differences (**bottom**).

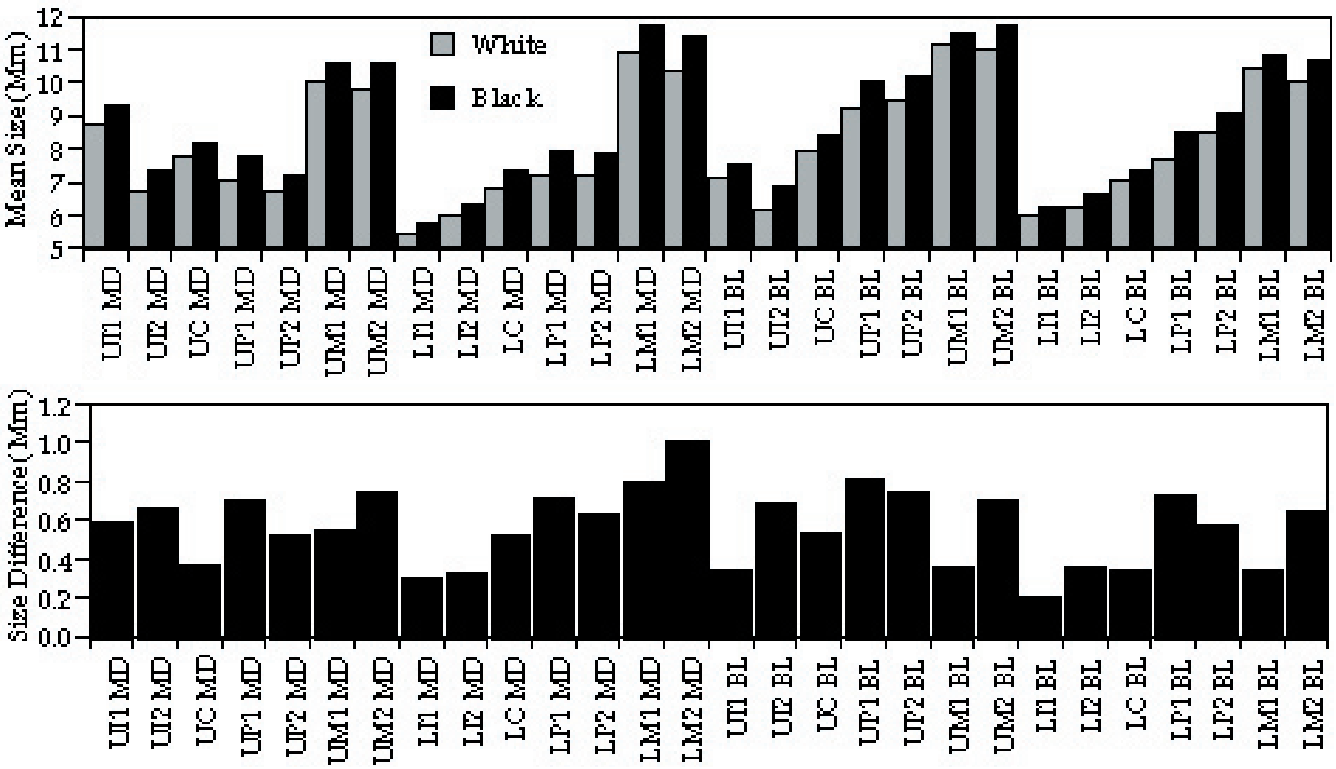

Fig. 5. Plot of crown dimensions by race (**top**) and black-minus-white differences in mean size showing that black have larger means throughout the dentition (**bottom**).

crown are largely coupled in terms of their ontogeny and genetic control. If these two commonly-measured axes of crown size (MD and BL) were not strongly related, one would expect appreciably more variance to be due to this contrast of measured dimensions. Researchers who have studied the genetic control of tooth size (*e.g.*, Sofaer *et al*., 1971; Potter *et al*., 1976; Townsend and Brown, 1978) have commented on differences between MD and BL dimensions, but the results often are inconsistent among studies, suggesting that sampling fluctuations may be at work.

The suggestion has been advanced that MD dimensions have lower heritabilities than BL dimensions because teeth compete for size of the dental lamina in the dental arch. In contrast, BL dimensions do not. This scenario seems to be insufficient as concerns a couple of developmental points. Teeth do not develop from the dental lamina—like beads on a string—instead, they develop from projections of condensed mesenchyme (i.e., the presumptive dental papilla) that extend away from the presumptive occlusal plane, with considerable space between them (Arey, 1965; Slavkin, 1974; Ooë, 1981). The tooth buds develop in a three-dimensional array such that, while their bony crypts may overlap mesiodistally, they are offset mediolaterally and craniocaudally (van der Linden and Duterloo, 1976; Duterloo, 1991). Teeth do not compete for space until their fully formed crowns erupt into the oral cavity where underdeveloped arch size may cause an arch-size to tooth–size discrepancy (Little, 1975). The high prevalence of crowding in contemporary westernized populations is a recent epidemiological problem that seems to be predominately acquired rather than inherited (Corruccini and Potter, 1980; Harris and Smith, 1980).

Sex

It is well documented that males have bigger teeth than females as statistical averages (*e.g*., Mijsberg, 1931; Gonda, 1959; Garn, 1966; Garn *et al*. 1964, 1967; Harris and Bailit, 1987), though the amount of sex difference is specific to a population, not a fixed effect (Hanihara, 1978). It is a bit surprising, then, that variance due to sex accounted for just 1.2% of the total variation in the present study (Fig. 6). On the other hand, humans are characterized by their trivial sexual dimorphism in tooth size compared to the great apes (*e.g*., Harvey *et al*., 1978; Swindler, 2002). Garn *et al*. (1967) showed that the canine was the most dimorphic tooth in humans, at 4-6% depending on the group studied, which pales against such nonhuman primates as Papio and Pan, where the canine is more than half again as large in males as in females. The issue should also be considered that univariate analysis tends to exaggerate sex differences because redundant male-female differences are included in each test (Potter, 1972).

Ditch and Rose (1972) used discriminant functions analysis to correctly determine sex in an average of

93% of their cases (depending on the set of variables analyzed), and Garn and coworkers (1977, 1978) arrived at similar success rates. Brown and Townsend (1979) reported lower correct allocations (*ca*. 75% or less) using data from aboriginal Australians—the same as reported by Hanihara (1979)—indicating that the degree of sexual dimorphism is not tied to the tooth sizes of a group *per se*.

In passing, researchers also have provided discriminant functions based on crown sizes of the primary teeth that correctly identify sex better than expected from chance (DeVito and Saunders, 1990; Tsutsumi et al., 1993) even though the primary teeth are much less dimorphic (Harris, 2001).

Position

Depending on their position within a morphogenetic field (I, P, M), teeth are labeled as "stable" or "variable" (Butler, 1939; Dahlberg, 1945). This dichotomy refers to the metric and morphological variation exhibited by a tooth. A stable, early-forming tooth is larger, possesses more and larger cusps and other crown features, and is less likely to be reduced in size or congenitally absent. These and other considerations led Dahlberg (1945, 1951, 1986) and others to characterize the "fields" of the human dentition (Fig. 7). Several studies have shown that the increased variability of distal "variable" teeth is due to *diminished* genetic control (*e.g*., Lundström, 1948; Alvesalo and Tigerstedt, 1974).

(As an aside, this study did not account for the apparent field reversal, where LI1 is more variable than LI2, which Kjaer (1980) attributes to the weak vascular supply in the mandibular midline because of the *symphysis menti*.)

The present study shows that position is a comparatively small axis of variation, estimated at 0.4%, making it the most trivial of the factors studied in this model. This also emphasizes the caveat (above) that estimating the relative sources of variation in the dentition is a different issue than whether particular teeth exhibit statistically significant differences. A key metrical attribute of a pole tooth within a field is its relative metric stability (Townsend and Brown, 1981). Coefficients of variation are graphed in Figure 8, where it is seen that it is not a foregone conclusion that the later-forming tooth possesses significantly great variance statistically. For the six contrasts in Figure 8, just three achieved significance ($\alpha = 0.05$ for one-tail tests). Just the maxillary incisors (I2 > I1) and the upper and lower molars (M2 > M1) exhibit significantly more variance in one tooth vis-à-vis the other. In all these instances, the distal tooth is always the more variable tooth.

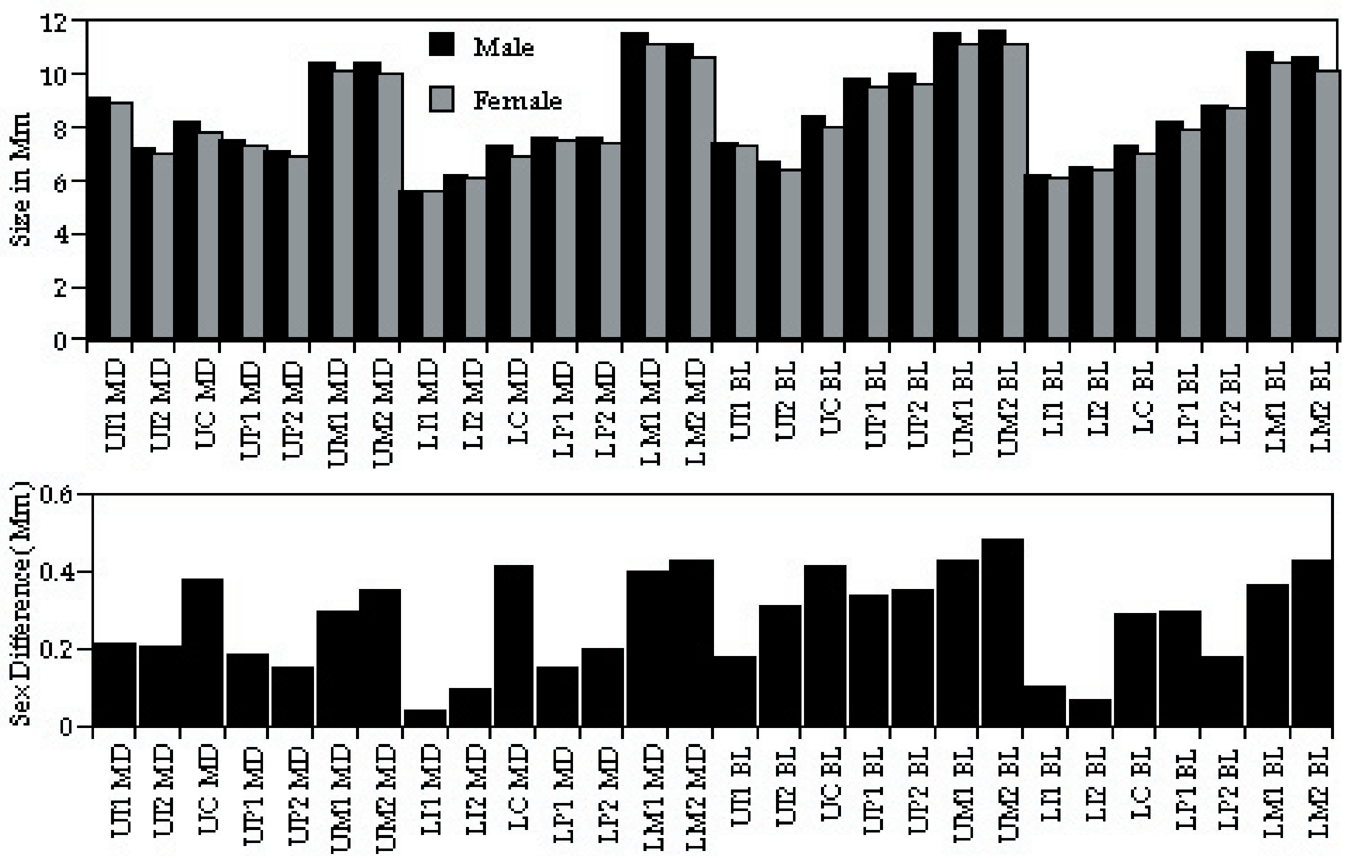

Fig. 6. Plot of tooth crown dimensions by sex (**top**) and plot of the male-minus-female differences (**bottom**) showing that, characteristically, males have larger mean crown dimensions.

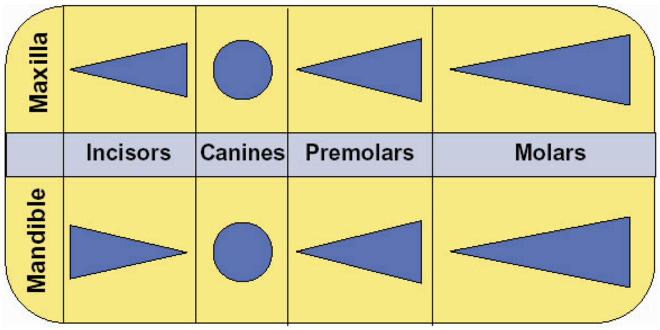

Fig. 7. Diagrammatic depiction of the morphogenetic fields in the human permanent dentition (modified from Dahlberg, 1951). The vertical height of the triangles reflects the variability of the distal tooth in each field. The exception is the 'reversed' field in the mandibular incisor region where the central incisor is more variable. There a mesial-to-distal gradient of increasing metric and morphological variation in the other fields (the stable canine obviously has but one tooth in each quadrant).

OVERVIEW

What are the major axes of variation in the permanent dentition in terms of tooth size? Results of the present study show that *the* canonical axis is among tooth types, which accounts for more than half of the variation (59%). There is a dramatic drop-off after tooth type is accounted for. Arcade (4.9%), race (3.5%), and crown dimension (2.6%) have only minor but comparatively intermediate values. Least influential are sex (0.9%) and tooth position within a field (0.4%). None of these axes of variation hinges on any one tooth, and the fundamental lack of more and more-prominent axes of variation is assumed to be due to the strong, pervasive statistical and developmental correlations among crown dimensions.

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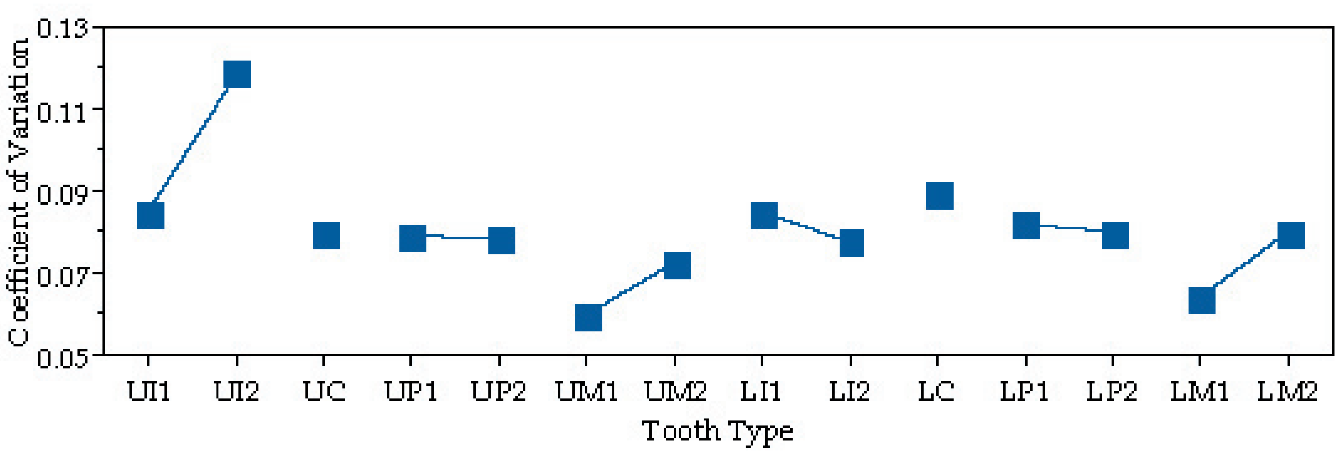

Fig. 8. Coefficients of variation by tooth type, having pooled across race, sex, and dimension (MD or BL). Line segments connect the stable and variable tooth within each morphogenetic field, but just three of the six comparisons disclose the anticipated mesial-to-distal increase in variability, namely UI1-to-UI2, UM1-to-UM2, and LM1-to-LM2.

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Want to know when your subscription to *Dental Anthropology* expires? Membership in the Association and, thus, your subscription to *Dental Anthropology* is on an annual basis coinciding with the calendar year. Have a look at the mailing label on the evelope that this issue arrived in, and you will see the year for which your dues have been paid. The year is located in parentheses to the right of your name. So, if the mailing label says "(2003)" you are paid to the end of this calendar year.

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telephone: (505) 277-4415
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CAPA Meeting

The annual meeting of the Canadian Association for Physical Anthropology will be held in Edmonton, Alberta, October 23-25 of 2003. Contributed papers and posters for a symposium on Dental Anthropology are welcome.

For further information, contact Dr. Nancy Lovell, Department of Anthropology, University of Alberta, Edmonton, T6G 2H4 Canada. E-mail: nancy.lovell@ualberta.ca

THE ALBERT A. DAHLBERG PRIZE: 2003

The Albert A. Dahlberg Prize is awarded annually to the best student paper submitted to the Dental Anthropology Association (DAA). **Submissions can now be sent for the 2003 competition**. Dr. Dahlberg was a professor at the University of Chicago, one of the founders of the International Dental Morphology Symposia, and among the first modern researchers to describe variations in dental morphology and to write cogently about these variations, their origins, and importance. The prize is endowed from the Albert A. Dahlberg Fund established through generous gifts by Mrs. Thelma Dahlberg and other members of the Association.

Papers may be on any subject related to dental anthropology. The recipient of the Albert A. Dahlberg Student prize will receive a cash award of $200.00, a one-year membership in the Dental Anthropology Association, and an invitation to publish the paper in *Dental Anthropology*.

Students should submit 3 copies of their papers in English to the President of the DAA. Manuscripts must be received by January 31, 2003. The format must follow that of *Dental Anthropology*, which is similar to the style of the *American Journal of Physical Anthropology* printed in 2003, Volume 120(1). The Guide to Authors also is available at the web site for the AJPA (http://www.physanth.org).

The manuscript should be accompanied by a letter from the student's supervisor indicating that the student is the primary author of the research and the paper. Multiple authorship is acceptable, but the majority of the research and writing must be the obvious work of the student applying for the prize. Send enquiries and submissions to the President of the DAA:

Dr. Joel D. Irish
Department of Anthropology
University of Alaska
Fairbanks, AK 99775-7720 U.S.A.
e-mail: ffjdi@uaf.edu

The winner of the Albert A. Dahlberg Student Prize will be announced at the Annual Meeting of the DAA, which is held in conjunction with the annual meeting of the American Association of Physical Anthropologists. In 2004, the meeting will be held in Tampa, Florida. The date, time and venue will be announced by the AAPA.

PLEASE ADVERTISE THIS COMPETITION TO YOUR STUDENTS

DAA SECRETARY-TREASURER CHANGE OF ADDRESS

Dr. Heather H. Edgar was elected the Association's Secretary-Treasurer at the Annual Meeting. Heather replaces Dr. Diane Hawkey who served with extreme competence and efficiency from 2000 to 2003. Diane has continued her duties into the Summer of 2003 to ease Heather's transition into this important and demanding job.

Heather is the person to be contacted with your annual dues and for any change of address. Her office address is:

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The Association is most appreciative of Diane's hard work and ability always to "stay on top" of a dynamic situation concerning the budget, membership list, and a host of other key ingredients that keep the Dental Association functioning. Likewise, we welcome Heather aboard as an elected official and hope her work progresses smoothly.

The Editor

Minutes of the 18th Annual Dental Anthropology Association Business Meeting—April 24, 2003, Tempe, AZ

<u>CALL TO ORDER</u>:
The meeting was called to order at 7:40 pm, by President Joel Irish. Forty members were in attendance.

<u>OLD BUSINESS</u>:
No items were discussed.

<u>**NEW BUSINESS:**</u>
1. Retirement of officers. Diane Hawkey ended her term as Secretary-Treasurer.

2. Election of new officer. One new officer was elected by unanimous vote: Heather Hecht Edgar (Secretary-Treasurer, 2003-2005).

3. AA Dahlberg Student prize. The winner of the 2003 AA Dahlberg Student Prize was awarded to Tomislav Lauc for his paper entitled *Influence of Inbreeding on the Carabelli Trait in Human Isolates*. He was able to attend through an International research development award from the Wellcome Trust, through Drs. Igor Rudan and Harry Campbell. He received $200.00, a certificate of award, a year's free membership in the DAA, and will have his article published in the journal. Honorable mention went to Heather Hecht Edgar for her paper *Dentitions, Distance, and Difficulty: A Comparison of Two Statistical Techniques for Dental Morphological Data*; the Honorable Mention award consists of a $50.00 cash award, certificate, a year's membership to DAA and publication of her article in the journal. Drs. Lauc and Edgar are pictured in Figure 1.

Fig. 1. Heather Edgar (*left*) and Tomislav Lauc, winners of the Dahlberg Student Awards for 2002.

4. AA Dahlberg Student Prize Contributions. On behalf of DAA, Irish thanked the individuals responsible for generous contributions to the fund, including Thelma Dahlberg and Stephen Hershey, and to numerous members who have contributed to the international sponsorship fund.

5. Editor's Report. Harris proposed that the journal be expanded to 4 issues a year, along with an increase in membership dues to help cover the cost of increased postage rates. Patricia Smith suggested that the DAA explore the possibility of online subscription. John Mayhall also mentioned some of the added benefits of making *Dental Anthropology* available online in PDF, including color photographs, and membership dues at a reduced rate (e.g. $20.00 PDF, $30.00 hard copy). After a lively debate, it was decided that the question of quarterly publication and a dues increase be addressed in the journal for membership vote.

6. Secretary-Treasurer'sReport. Hawkey reported that as of April 24th, the DAA has $2,395.23 in the 2003 operations budget, and $2,403.40 in the AA Dahlberg Prize Fund. We have a total of 273 members (101 are international, 172 are U.S.). She noted that DAA student membership appears to be decreasing–only 17.6% of current DAA members are students (9 international students, 39 U.S. students, 92 international regular membership, 133 U.S. regular membership.)

7. Additional topics. Phil Walker had made a suggestion earlier at the DAA Executive Committee meeting that DAA apply to be included in Index Medicus, which would also give the association increased recognition. Alma Adler volunteered to be the new DAA Webmaster and Patricia Smith offered a CD-ROM tooth identification program developed at Hebrew University for inclusion on the new website. Sue Haeussler mentioned a recent letter received from Thelma Dahlberg with her best wishes for the association. Kudos were given to Heather Hecht Edgar and Loren Lease (co-Chairs) and Simon Hillson (Discussant) for their work on this year's DAA-sponsored poster symposium that was titled "Morphometric Variation in the Dentition of Modern Homo sapiens" but was known colloquially as "More Teeth Than You Can Shake a Stick At".

<u>ADJOURNMENT</u>:
The meeting was adjourned at 8:12 pm by Irish, allowing members time to further socialize at the DAA cash bar.

Submitted by: Diane E. Hawkey
DAA Secretary-Treasurer

NOTICE TO CONTRIBUTORS

Dental Anthropology publishes research articles, book reviews, announcements and notes and comments relevant to the membership of the *Dental Anthropology Association*. Editorials, opinion articles, and research questions are invited for the purpose of stimulating discussion and the transfer of information. Address correspondence to the Editor, Dr. Edward F. Harris, Department of Orthodontics, University of Tennessee, Memphis, TN 38163 USA (e-mail: eharris@utmem.edu).

Research Articles. The manuscript should be in a uniform style (one font style, with the same 10- to 12-point font size throughout) and should consist of seven sections in this order:

Title page	Tables
Abstract	Figure Legends
Text	Figures
Literature Cited	

The manuscript should be double-spaced on one side of 8.5 x 11′′ paper (or the approximate local equivalent) with adequate margins. All pages should be numbered consecutively, beginning with the title page. Submit three (3) copies—the original and two copies—to the Editor at the address above. Be certain to include the full address of the corresponding author, including an e-mail address. All research articles are peer reviewed; the author may be asked to revise the paper to the satisfaction of the reviewers and the Editor. All communications appear in English.

Title Page. This page contains (a) title of the paper, (b) authors' names as they are to appear in publication, (c) full institutional affiliation of each author, (d) number of manuscript pages (including text, references, tables, and figures), and (3) an abbreviated title for the header.

Abstract. The abstract does not contain subheadings, but should include succinct comments relating to these five areas: introduction, materials, methods, principal results, and conclusion. The abstract should not exceed 200 words. Use full sentences. The abstract has to stand alone without reference to the paper; avoid citations to the literature in the abstract.

Figures. One set of the original figures must be provided with the manuscript in publication-ready format. Drawings and graphics should be of high quality in black-and-white with strong contrast. Graphics on heavy-bodied paper or mounted on cardboard are encouraged; label each on the back with the author's name, figure number, and orientation. Generally it is preferable to also send graphs and figures as computer files that can be printed at high resolution (600 dpi or higher). Most common file formats (Windows or Macintosh) are acceptable; check with the Editor if there is a question. The journal does not support color illustrations. Print each table on a separate page. Each table consists of (a) a table legend (at top) explaining as briefly as possible the contents of the table, (b) the table proper, and (c) any footnotes (at the bottom) needed to clarify contents of the table. Whenever possible, provide the disk-version of each table as a tab-delimited document; do not use the "make table" feature available with most word-processing programs. Use as few horizontal lines as possible and do *not* use vertical lines in a table.

Literature Cited. *Dental Anthropology* adheres strictly to the current citation format of the *American Journal of Physical Anthropology*. Refer to a current issue of the *AJPA* or to that association's web-site since the "current" style is periodically updated. As of this writing, the most recent guidelines have been published in the January, 2002, issue of the *AJPA* (2002;117: 97-101). *Dental Anthropology* adheres to the in-text citation style used by the *AJPA* consisting of the author's last name followed by the year of publication. References are enclosed in parentheses, separated by a semicolon, and there is a comma before the date. Examples are (Black, 2000; Black and White, 2001; White et al., 2002). The list of authors is truncated and the Latin abbreviation "et al." is substituted when there are three or more authors (Brown et al., 2000). However, *all* authors of a reference are listed in the Literature Cited section at the end of the manuscript.

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